

Reproduction and survival in Common Buzzards (*Buteo buteo*) illustrated by the seasonal allocation of energy expenses

Magnus Sylvén



Department of Animal Ecology
University of Lund, Sweden
Lund 1982



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TACK

Staffan Ulfstrand och Sam Erlinge har båda fungerat som mina handledare under studietiden. Staffan engagerade sig i mitt intresse för ormvråkar även före min tid på Ekologihuset. Till dessa båda riktas ett innerligt tack både för frikostig resurstilldelning under årens lopp, fortlöpande engagemang samt slutliga kommentarer i samband med avhandlingens skriftliga tillblivelse.

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Dick Forsmans ormvråk pryder omslaget. Tack vare Astrid Ulfstrands förnämliga vinjetter, har flera tråkiga figurer fått en välbehövlig ansiktslyftning. Steffi Douwes har framställt samtliga figurer på ett snabbt och föredömligt sätt, ibland utifrån mindre lyckade original. Slutlig utskrift av texten har gjorts av Ulla Holmberg, medan Ylva Zachrisson och Anne Odham renskrivit tabellerna. Gunilla Lindquist har gjort slutredigeringen. Som fältassistenter har tjänstgjort Ulf Sandnäs, Åke Persson och Staffan Widstrand.

Till alla dessa människor framför jag mitt stora tack. Slutligen vill jag rikta mig med tacksamhet till Per Brinck, institutionens överhuvud under alla dessa år. Hans arbete har möjliggjort att nödvändiga basresurser alltid funnits tillgängliga.

INTRODUCTION

As part of a project dealing with the impact of mammalian and avian predators on small rodents in southern Sweden, a Common Buzzard population was studied during a six year period (1975-80). Both the diet and the breeding performance of the population were monitored during this period (paper I). In 1975-76, the monthly activity pattern of adult buzzards was studied mainly in four territories, where individual recognition was possible through wing tagging or plumage features (paper II). Special emphasis was paid on the behaviour during the breeding season, especially its earliest part, when the males feed their mates during egg formation (paper III). Finally, the interspecific relations between Common and Rough-legged Buzzards were studied in the winter 1975/76 (paper IV).

A characteristic feature of the study area is the occurrence of non-cyclic rodent populations. The annual production of both Field Voles, Microtus agrestis, and Wood Mice, Apodemus sylvaticus, equals the estimated annual vole and mouse consumption by the predators. The Common Buzzard plays a dominant role in this predation, especially due to its high density in the area (Erlinge et al. 1982).

In mid-April each year, the buzzards initiate egg laying. This coincides with a period when the voles, much due to predation, nearly have reached their lowest numbers of the year. In spite of this, the buzzards were found to base a substantial part of their egg production on Field Voles, probably because alternative prey species were lacking. Frogs were, however, found to constitute an important complement.

During the egg formation period, the female buzzard stops hunting and is entirely fed by her mate for nearly two weeks. By this she loses, however, the possibility to obtain food by her own hunting. Had she spent a time hunting that was only half the hunting effort of the male, she probably would have gained extra energy corresponding to the cost of forming two eggs or to the accumulation of about 13 g fat each day (provided the male would still have fed her at the same rate). That the female buzzard refrains from such profits probably has two reasons: (1) she eliminates the risk of damaging the developing eggs within her body when hunting, and (2) as soon as egg laying has started, she reduces the risk of losing the clutch to predators. This adaptation, however, exposes the buzzards to considerable risks of early nest failure due to e.g.

unfavourable feeding conditions early in the breeding season. In agreement with this, early failures dominated, and much of the variation in breeding success between years was due to the performance at this stage.

One might wonder why the buzzards start breeding so early. Why do they not postpone egg laying to a more favourable time later in spring, when the food situation has improved considerably? The background may be that (1) by starting early, the buzzard fledglings face an extended period of favourable food conditions late in summer, and (2) the parent buzzards increase their chances to survive the winter. Timing of egg laying has probably evolved to allow time both for moult and fattening before winter. The start of moult is closely connected with the start of breeding, female buzzards usually initiating moult already during incubation, males starting approximately one month later. If buzzards postponed their egg laying about six weeks to a period when, for instance, young Rabbits emerge from their burrows, the moult would not be completed until late autumn. The amount of extra energy needed for feather replacement would probably diminish total fat deposition by approximately 86% in males and by 73% in females. This would almost certainly put their winter survival at a risk.

However, once beyond the initial difficulties, reproductive performance improves. Both hatchability and nestling survival were constantly high. Very few losses of whole broods occurred at this stage (most of them due to accidents, e.g. nests blown down in strong gales). In this period, the diet is markedly different from that in spring. In the first two years of the study when Rabbits were abundant, young Rabbits dominated the prey brought to the nestlings. But during a succession of unfavourable winters, the Rabbit population declined. Although this caused an increase in the diversity of prey brought to the nestlings, it did not have any apparent influence on nestling survival. The availability of alternative prey species helped the buzzards to keep nestling survival constantly high.

Those buzzard pairs occupying areas with the highest output of young Rabbits and Field Voles, produced most young. The most productive clutch size in the population (4 eggs) was not the same as the commonest one (3 eggs). A positive correlation between number of eggs laid and offspring production existed, thus conflicting with Lack's ideas from 1947-48. The fundamental assumption behind this postulate was that clutch size is to a large

extent inherited. However, the very few studies up to date, that have tried to determine the genetic influence on clutch size in birds do not strongly support this idea. In the Great Tit, Parus major, Nordwijk et al. (1980) found a heritability value of about 40%, while Högstedt (1980) found that territory quality accounted for about 85% of the within-year variation in clutch size in the Magpie, Pica pica, and that only about 15% could be attributed to differences between females. So for the moment, it is probably wise to conclude that "an individual female merely inherits the ability to vary the clutch size within a certain range, while the actual number laid on any occasion is determined phenotypically (Jones & Ward 1976)". Each buzzard pair seems to adapt the clutch size to available resources in the territory, and my results seem to confirm the conclusion that "territory quality is the most important factor to determine the optimal clutch size in territorial birds" (Högstedt 1980).

In at least two breeding seasons, when the Buzzards lived mainly on young Rabbits, they probably did not realize their maximum breeding potential. Although the male alone provided most of the food during the nestling stage, he hunted very little. His daily energy expenditure ($2.7 \times \text{BMR}$) was much lower than the possible maximum ($4 \times \text{BMR}$, Drent & Daan 1980). To interpret this, however, as being an adaptation to decrease the reproductive cost in order to increase adult survival and thereby lifetime reproduction (Williams 1966, Charnov & Krebs 1974) seems unnecessary. It is more likely that the birds were unable to realize their breeding potential because food was limited during egg laying. Before and during egg laying, voles and frogs dominated the diet whereas during the nestling stage Rabbits were the most important prey.

Juvenile buzzards were found to survive the post-fledging period extremely well. In 14 broods, containing 34 young, no single loss was registered during two months. This period coincides, however, with a favourable food situation, since young voles are continuously produced until the end of summer.

Thereafter, the juveniles start dispersing from the area, and in late autumn most of them seem to have reached Denmark and northern Germany. One winter recovery also comes from Holland.

During the autumn, adult buzzards start putting on fat for the winter period. The female maximizes her deposition earlier than the male, probably because she is able to finish moult approximately one month ahead of the male. By this she accumulates

both higher relative and absolute amounts of fat. This deposition helps her to buffer unfavourable food conditions during winter better than the male is able to, and accordingly, females survive the winter better than males. January is the month when both male and female buzzards have to maximize food intake, not because of high activity level, but due to the few hours of daylight available to them.

In winter, the resident pairs have to defend their territories not only against conspecifics but also against Rough-legged Buzzards. The resident pairs, however, are able to establish winter territories at an early stage, using the most favourable vole habitats within their summer ranges and leaving the rest of the area to immigrants.

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I will, however, end this introduction by presenting an attempt at a synthesis of why female raptors are often larger than their mates and why this size dimorphism is more pronounced in some species than in others. The first and the third paper of this thesis provide a background. The reason for presenting these ideas in the introduction is twofold. Firstly, the paper is mainly based on ideas put forward by others, although I was stimulated to write about this problem by some of my own experiences from the buzzard study. Secondly, I think it contrasts too much with the unit of the rest of the thesis to be presented separately. But since the problem of the reversed size dimorphism has had such an impact on much

of the writings on raptor ecology during the last ten years, I find the issue tempting. This question also illustrates the importance of having a deep insight into the ecological adaptations of different species. Only with this background, are we likely to understand an adaptation like the reversed size dimorphism in raptorial birds.

SELECTION FOR FOOD SEGREGATION BY REVERSED SEXUAL SIZE DIMORPHISM IN RAPTORIAL BIRDS

In recent decades, a series of explanations have been put forward why female raptors usually are larger than males, and why the size difference is more pronounced in some species than in others. Extensive reviews have been published by Snyder & Wiley (1976), Newton (1979), Walter (1979) and Andersson & Norberg (1981). In spite of this, I will present a slightly different interpretation from those of earlier authors, although I base it mainly on ideas put forward by others. Essentially it is a synthesis of some of the earlier interpretations. My basic assumption is that the evolution of a pronounced size dimorphism in raptorial birds should mainly be regarded as a result of the selection for increased offspring production brought about by extending the joint food niche of the pair. Thus I adopt the view of several previous authors (e.g. Snyder & Wiley 1976, Andersson & Norberg 1981). I start with the question why female raptors usually are bigger than their mates. Thereafter I discuss the degree of size dimorphism found in different raptors. The outline of this section is given below.

*Selection
for
Food segregation by
sexual dimorphism*

*No/weak Selection
for
Food segregation by
sexual dimorphism*

*Limited breeding resources
Exclusive food resources
(solitary breeding)
Wide food spectrum
Weak interspecific competition*

*A. Surplus of breeding resources
(limited survival resources)
B. Limited breeding resources
Colonial breeding/social foraging
Narrow food spectrum
Strong interspecific competition*

As a prerequisite, I assume that food partitioning in raptorial birds is mainly based on the development of a difference in body size, not on a difference in bill morphology, as has been suggested for many passerines (Schoener 1965).

WHY ARE RAPTOR FEMALES LARGER THAN THE MALES?

Probably to avoid the risk of damaging the developing eggs when hunting (Walter 1979) and to prevent egg predation during the egg laying period (Hunt 1980), female raptors refrain from hunting and are fed by their mates early in the breeding season (see Sylvén 1982c). In species which exploit predictable food resources and where harvesting efficiency increases if current hunting information is always available to the same individual, it is probably more profitable with permanent roles during incubation and when the nestlings need to be brooded (Alerstam & Högstedt 1982): the female incubates and broods and the male provides food. Examples of such species are most raptors feeding on mammals and birds. With permanent roles, larger females are better adapted for nest defence than smaller ones (Andersson & Norberg 1981), and since the male's role in nest protection is slight, this results in development of larger females than males. This nest defence argument, originally proposed by Storer (1966), seems to be embraced by an increasing number of spokesmen in recent years (e.g. Reynolds 1972, Snyder & Wiley 1976, Newton 1979, Andersson & Norberg 1981).

For species relying on food sources that are unpredictable in time and space and where information from earlier hunts is of little value, the benefit of permanent roles during incubation and early brooding is probably small. Good examples are most carrion-living vultures (both New and Old World species) and many insectivorous raptors, e.g. Falco vespertinus and F. naumanni. In these species, both sexes participate in incubation more or less equally (see e.g. Brown & Amadon 1968, Newton 1979, Cramp et al. 1981), and in none of them is the female larger than the male (in some of the vultures, the reverse is actually true!). Here, selection for nest defence efficiency works equally on both sexes.

Several other explanations for the evolution of reversed sexual size dimorphism in raptorial birds have been put forward. Many of them are discussed in detail by Snyder & Wiley (1976), Newton (1979), and Andersson & Norberg (1981); I will only mention a few.

Larger females probably produce larger eggs (Reynolds 1972) and incubate more efficiently (Snyder & Wiley 1976) than do smaller females. But both these arguments apply to all kinds of birds, not only to raptors

Ricklefs' (1974) conclusions, that the relationship between egg weight and female body weight increases faster with increasing female weight in passerines than in non-passerines, made von Schantz & Nilsson (1981) put forward the hypothesis, that the larger female size in raptors can be seen as a result of a selection to reduce the relative costs for egg laying in such birds. However, courtship feeding is characteristic during the egg formation period in most raptors (Newton 1979) and the male is mainly responsible for whether egg laying will be realized or not. From an energetic point of view, it would be more profitable for a male to feed a small female who lays relatively large eggs than to feed a large female who lays small eggs. For efficient egg laying it is important to minimize the absolute energy expenditures, not the relative costs. Therefore, this explanation seems to be less promising.

THE DEGREE OF REVERSED SIZE DIMORPHISM

a. SOLITARY BREEDING VERSUS COLONIALITY

Probably the most important ultimate reason why pronounced sexual dimorphism evolved in raptorial birds is that it enables an enlargement of the combined food base of the pair during breeding resulting in more offspring being produced. This restricts possibilities for developing pronounced size dimorphism to species living on more or less exclusive food resources, either they live in feeding territories, like most Buteo species (Newton 1979), or their nests are fairly regularly spaced in order to diminish mutual interference between pairs (Nilsson et al. 1982), as in many Accipiter populations (Newton et al. 1977).

In most colonial species, size dimorphism has little opportunity to evolve since the individuals exploit a common food resource. In at least several such species, both sexes also participate more or less equally in the incubation and in the brooding of small young (the carrion-living vultures and the insectivorous falcons mentioned earlier are good examples). So, the exploitation of a common food resource and the lack of permanent roles in the first half of the breeding period, give bad prerequisites for the development of a pronounced reversed sexual size

dimorphism in many colonial raptors. These are probably the two most important reasons for the low frequency of size dimorphism that characterizes many gregarious raptor species (for the generally small size dimorphism in such species, see Walter 1979).

b. LIMITING PERIODS OUTSIDE THE BREEDING SEASON

Birds, whose populations are mainly limited by the carrying capacities of survival habitats and where competition is strong and mortality considerable outside the breeding season, probably have small opportunities to realize a strong sexual size dimorphism in order to increase the pair's food niche in the breeding season. This applies to most small-sized terrestrial birds (Alerstam & Högstedt 1982). At the other end we find species with a surplus of survival habitats and weak competition and low mortality, such as most sea-birds (Alerstam & Högstedt 1982). Here we would perhaps expect to find numerous examples of well developed sexual size dimorphisms had it not been that many species are extremely gregarious and breed in huge colonies, where both intra- and interspecific competition is intense (Buckley & Buckley 1980), the territorial skuas constituting the only exception. Most raptorial birds occupy a position somewhere between these extremes (Alerstam & Högstedt 1982), giving them a fairly good chance to develop sexual size dimorphism.

c. FOOD STRESS DURING BREEDING

The only period in which individuals of a species can benefit from diverging in size, thus enabling them to exploit different parts of the food spectrum, is the time when both members of the pair hunt, generally at the end of the breeding cycle. If this period is critical, and if an enlarged food niche would improve the parents' ability to raise young, then a sexual size dimorphism could evolve, provided that other ecological conditions permit. Since the large body size of the female is coupled to nest defence, the only way to increase the exploitation of available resources is for the male to become smaller.

Snyder & Wiley (1976) emphasized that knowledge of the seasonal variation in food availability is essential for the understanding of the evolution of size dimorphism in raptors. "The differences in prey availability curves for raptors feeding on birds, mammals, and insects may give rise to different intensities of selection

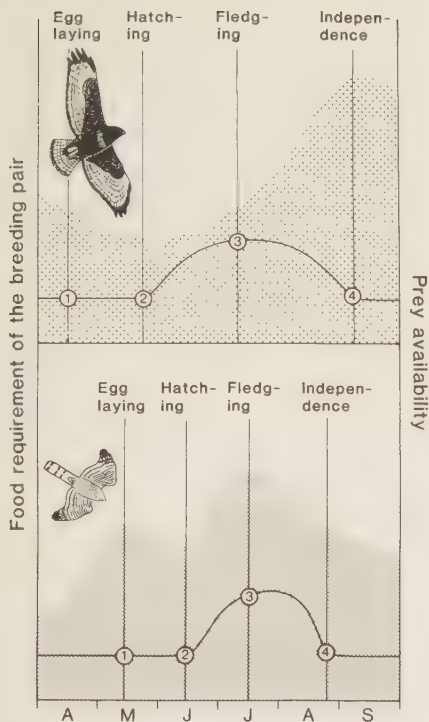


Fig.1. Conditions of prey availability (shaded areas) for a raptor species living on small rodents (upper) and on small birds (lower) in temperate regions. The figure is based on an idea of Snyder & Wiley (1976). The small mammal situation is illustrated by the Common Buzzard *Buteo buteo* (σ 790 g, η 990 g) while the Sparrowhawk *Accipiter nisus* (σ 145 g, η 265 g) illustrates the situation for a raptor living on small birds. The increase in food availability for the rodent-eating buzzard in the second half of the breeding season is due to reproduction in the vole population. The first food peak in prey availability for the Sparrowhawk is due to the flow of migrant birds passing through the breeding area in late spring and the latter peak corresponds to the output of passerine fledglings. The curves indicate the food requirement of a pair with nestlings (for the buzzard, based on Sylvén 1982 a).

for dimorphism". The regularity with which a raptor species is stressed by food shortage late in the breeding cycle may be the most important factor (Snyder & Wiley 1976).

Fig. 1 illustrates the seasonal availability of prey for temperate raptors living on small mammals and on small birds, respectively. For a buzzard, the fledgling dependency period coincides with a general increase in prey availability. Young buteos have been found to develop hunting skill rather quickly, already within the post-fledging period (Snyder & Wiley 1976, Newton 1979); the favourable food situation at this late stage means that the need for the parents to widen their common food niche by differentiating in size is slight.

In contrast, young accipiters generally remain dependent for a more extended period before developing their hunting skill than do rodent-eating raptors (Snyder & Wiley 1976, Newton 1979). Because food availability declines in the latter part of the breeding season (Fig. 1), raptors feeding on birds can probably bene-

fit more from enlarging the food base by separating in size than can mammal-feeding species.

The situation for insectivorous raptors is less clear, but according to several sources cited by Snyder & Wiley (1976), at least insect populations belonging to the orders Orthoptera, Coleoptera, and Lepidoptera have seasonal trends resembling the typical mammal situation. Therefore, also for insectivorous raptors, it is doubtful if an increased size dimorphism could really increase the food spectrum of the pair. The available prey is anyhow so small compared to the body size of the raptor (Snyder & Wiley 1976, Andersson & Norberg 1981).

d. ADVANTAGES OF SIZE DIMORPHISM

The benefits of niche segregation between the sexes during the breeding season may be twofold: (1) when both parents provide food for their young, each sex feeds from a part of the food spectrum not exploited by the other (Snyder & Wiley 1976), and (2) hunting by the male early in the breeding season, when the female refrains from hunting, does not reduce the later availability of prey for the female (White & Cade 1971, Andersson & Norberg 1981). Both factors may help to enlarge the combined food base of the pair and increase offspring production. Their selective advantage will increase progressively when prey availability decreases.

A diet difference between the sexes at the end of the breeding cycle has been demonstrated in various moderately to strongly dimorphic raptor species (for a review, see Newton 1979).

In spite of the tremendous hunting effort needed late in the breeding period, the feeding rate of male Sparrowhawks Accipiter nisus (Newton 1978, Perrins & Geer 1980) and male Sharp-shinned Hawks, A. striatus (Snyder & Wiley 1976) has been found to decline markedly in some pairs at this stage. This has been interpreted as being mainly the result of decreased prey availability for the males. In such situations, the female is entirely responsible for the provisioning during the final stage of the breeding cycle. If, at this time, she can start exploiting a prey largely unaffected by the male's earlier hunting, this would certainly be advantageous. The hunting by male Sparrowhawks has namely been found to substantially reduce the output of Great Tits, Parus major, within the neighbourhood of Sparrowhawk nests due to the predation on adult birds (Perrins & Geer 1980).

During the period when the male alone is responsible for the

hunting, it is not obvious that he benefits from being small, as has been suggested by Storer (1966) and further elaborated by Reynolds (1972) and von Schantz & Nilsson (1981). Thus, Snyder & Wiley (1976) found no support for this idea which is based on the assumption that the small size of the male is a result of "the pyramid of prey numbers". After an extensive survey of the distribution of biomass of different size classes in 65 breeding bird communities in North America, they summarized their analysis by: "we view the assertion that there might be generally more prey biomass available for male Sharp-shinned Hawks than for females as highly questionable. Available evidence suggests that the reverse is true". It is also disputable whether a frequent supply of small prey items has much advantage over an infrequent supply of large prey (Newton 1979).

e. CONDITIONS PROMOTING SIZE DIMORPHISM

Within a given geographical area, there seems to be many more species of birds than of mammals. In Northern Europe, about 230 bird species breed regularly compared to 58 species of mammals (Fig 2). If we restrict the view to size classes generally exploited by predatory birds (Fig 2), corresponding figures are 222 and 38, respectively. This pattern holds also for different habitats (Fig 3). So, generally speaking, raptors living on birds seem to have better opportunities than mammal-feeding species to prey on alternative species within the same area and thereby subdivide the utilization of their food resources.

There is probably also a progressive reduction of interspecific competition as one moves from exploiting slow-moving to fast-moving prey (Newton 1979). Carrion and insects are eaten by many different kinds of animals, living mammals by fewer, and fast-moving prey by very few predators. This probably allows a higher degree of food partitioning in raptor species feeding on birds than in raptors living on mammals, insects, or carrion (Newton 1979).

The more a predator depends on flight skill for prey capture, the more important is the ability to match the movement performance of the prey (Andersson & Norberg 1981). Because birds are extremely agile, a bird predator can hunt efficiently only within a limited range of prey sizes (Howland 1974, Andersson & Norberg 1981). For predators hunting less agile prey, the size of the predator relative to the prey is probably less important. If an enlarged food base is necessary to cope with adverse food condi-



Fig.2. Number of bird species (excluding diurnal raptors) and mammal species in northern Europe in different size classes. The figure illustrates the summer situation. Species belonging to size classes over 2.56 kg are considered less available to most raptorial birds. Data for birds are from Haftorn (1971) and for mammals from Siivonen (1975).

tions late in the breeding season, then a small male who hunts fast-moving prey like birds reduces the female's food spectrum less and competes with the female to a smaller extent than does a bigger male.

SUMMARY

The ideas developed in the foregoing sections can be summarized in five points.

- (1) To avoid damaging the developing eggs when hunting and to prevent predation on the eggs when laying has started, female raptors refrain from hunting and are fed by their mates. Incubation and early brooding is accomplished by the female alone in species where the prey of the nesting area is more efficiently exploited by one bird than by both sexes in succession. The permanent roles promote an increase in female body size as an insurance against nest predation.

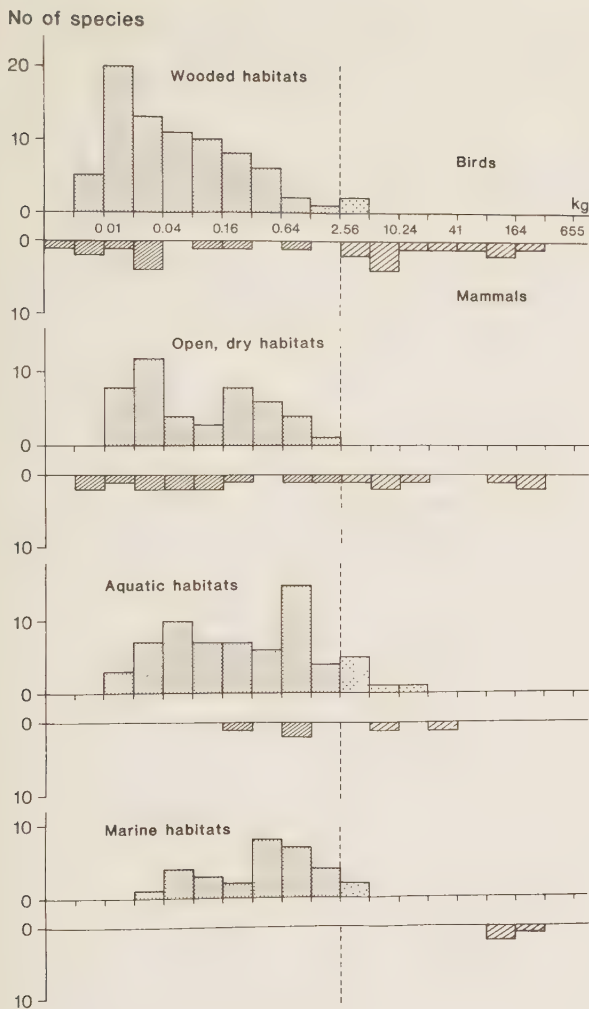


Fig.3. Habitat related distribution of bird and mammal species in different size classes in northern Europe. Data from the same sources as in figure 2.

In many gregarious raptors, which lack a permanent division of roles during the early part of breeding and which live on more unpredictable food resources (often exploited socially), selection for nest defence efficiency works equally on both sexes.

- (2) The ultimate reason for the evolution of a pronounced sexual size dimorphism in raptorial birds is probably that it enables the breeding pair to enlarge its food base and thence offspring production. This can be accomplished most efficiently

by birds breeding solitarily, exploiting a more or less exclusive food resource, and which are not seriously limited in the non-breeding season by food shortage due to interspecific competition.

- (3) The regularity with which raptor species are stressed by food shortage late in the breeding season is probably the most important factor influencing the degree of dimorphism. Information from temperate areas indicates that bird-eaters are often confronted with a decreasing availability of food late in the breeding season while raptors living on small mammals and insects are not.
- (4) Niche segregation between the sexes during the breeding season increases the pair's potential to exploit the available food resources of the nesting area. That the male exploits a part of the food spectrum different from that of the female probably also means that he does not affect the availability of prey for the female when she starts hunting at the end of the breeding cycle.
- (5) Due to a generally higher diversity of birds than of mammals within a given geographical area and to less interspecific competition among raptors living on fast-moving compared to slow-moving prey, raptors living on birds have better opportunities than mammal-feeding species to achieve partitioning of food between the sexes. An effective niche segregation can, however, only be realized by the sexes diverging in body size.

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OFFSPRING PRODUCTION OF COMMON BUZZARDS, Buteo buteo, IN RELATION
TO TIMING, AND LOCAL AND SEASONAL VARIATIONS IN FOOD SUPPLY.

ABSTRACT

The breeding performance in a Common Buzzard population was studied during six years in southern Sweden. Early breeding failures dominated. Both hatchability and nestling survival was constantly high, and juveniles survived the post-fledging period extremely well. Timing of egg laying was significantly influenced by spring temperature, whereas the influence of food supply was uncertain since the spring abundance of one of the main prey species, the Field Vole, did not vary significantly between years. Start of laying did not significantly influence clutch size or brood size at the time of fledging.

Offspring production was directly determined by number of laid eggs, which in turn was related to the local food supply. Considerable variations in the composition of prey brought to the nestlings did not have any apparent influence upon nestling survival.

1. INTRODUCTION

This paper deals with the breeding performance of a Common Buzzard, Buteo buteo, population in southern Sweden during six years. It describes the timing of reproduction, its proximate control, ultimate background, and consequences, especially in relation to seasonal variations in food supply. The reproductive output coupled to clutch size, local productivity of prey, and the parents' ability to raise young to fledging and independence is also examined. Data on nest dispersion, winter and summer territoriality, juvenile dispersal, adult residency and mortality are reported.

2. STUDY AREA AND METHODS

The study area, about 45 km² and situated in the southernmost part of Sweden (55.42°N, 13.25°E), mainly consists of cattle-grazed permanent grassland, interspersed with coniferous plantations, copses of deciduous trees, and marshes. The area offers an exceptionally diverse prey fauna. The drier parts are inhabited by Rabbits, Oryctolagus cuniculus, and the wetter areas primarily by Field Voles, Microtus agrestis, and Water Voles, Arvicola terrestris. These species constitute the three most important prey categories for the buzzard population (Sylvén 1978, and in prep.).

In March each spring, approximately 31 km² of the area were searched for territorial pairs and nest sites. From the end of April, known nests were inspected regularly. In two years, fledglings were also studied to determine survival during the period of parental dependence.

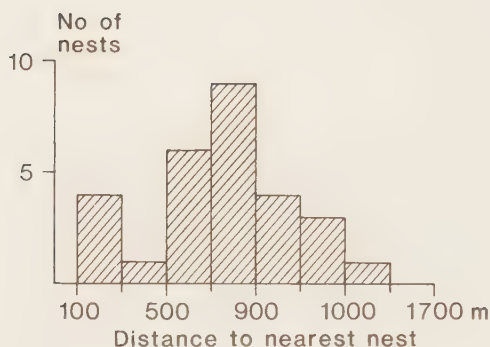


Fig.1. Closest distance between neighbouring Common Buzzard nests in southern Sweden.

Time of egg laying in most cases was estimated by back-dating from dates of hatching or from weights of small young. Initial egg weights were mostly calculated assuming a linear weight loss of, in total, 15% (Mebis 1965) during 34 days of incubation (Mebis 1964a). Nest inspections during the egg and nestling stage also gave some information about food choice.

Individual identification was facilitated by patagial tags on some buzzards, while in other cases plumage features were distinct enough to allow individual recognition.

To study the influence of local food supply on breeding performance, 15 territories were selected from which data on the number of fledglings had been obtained during at least two seasons. The analysis had to be limited to brood sizes since data on clutch sizes were inadequate. Since territory boundaries were usually not known precisely, I used an arbitrary "territory" covering a circle of 1 km radius around each nest. This entails a certain error, since the nest was sometimes situated near the periphery of the activity range. Habitat related densities and productivities were used to estimate the abundance of Field Voles around each nest (S. Erlinge, pers.comm.). Data on the distribution of optimal Rabbit habitats within the study area and on the production of young Rabbits were obtained from G. Jansson (pers.comm.).

3. POPULATION CHARACTERISTICS

3.1. NEST DISPERSION

During 1975-1980, nest sites within 28 territories were located. The mean shortest distance between neighbouring nests was 750 m (Fig. 1). Nests were fairly regularly spaced (Nilsson et al. 1982).

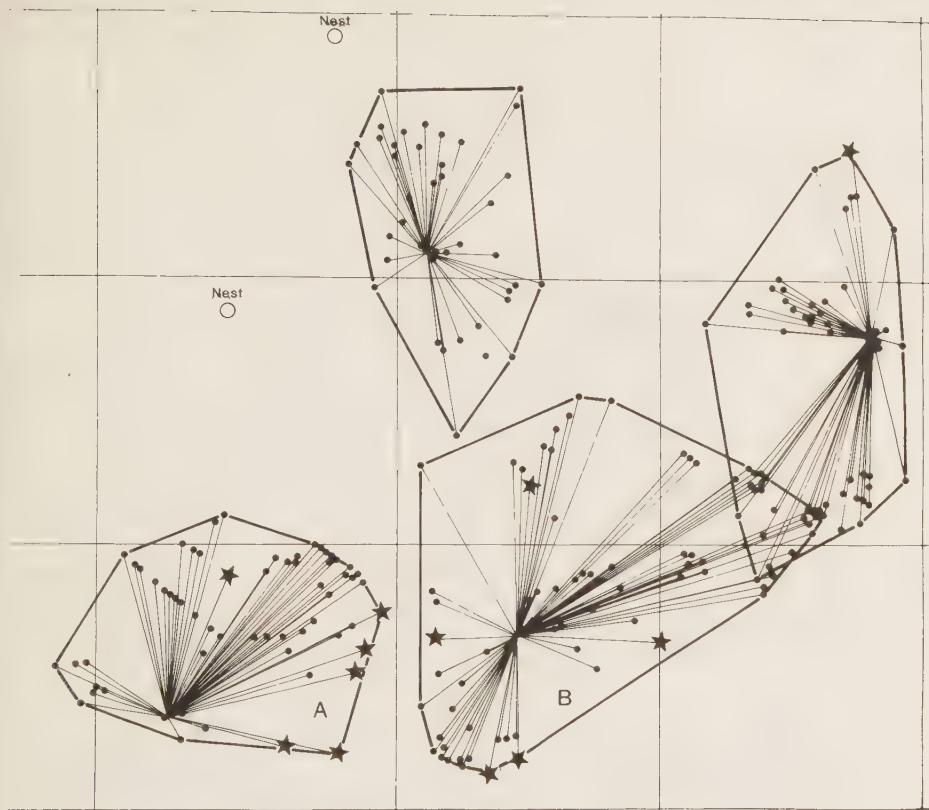


Fig.2. Hunting ranges of Common Buzzards breeding in southern Sweden. Different perch sites radiating from the nests and used during three consecutive years are combined. Many hunting perches were frequently in use every season. Stars show the position of interference between neighbours. The location of other buzzard nests is also shown. For pairs denoted A and B, the winter situation is illustrated in Fig.3. Each square represents one square kilometre.

3.2. TERRITORIALITY

As in most other studies of Buteo populations (Newton 1979), the buzzards were found to occupy territories. In the breeding season, much of the available space was covered by territorial pairs exploiting almost the same area from year to year (Fig 2). In winter, territorial pairs usually occupied a smaller part of their summer range (Fig 3), defending these areas not only against conspecifics but also against Rough-legged Buzzards, Buteo lagopus (Sylvén 1978).

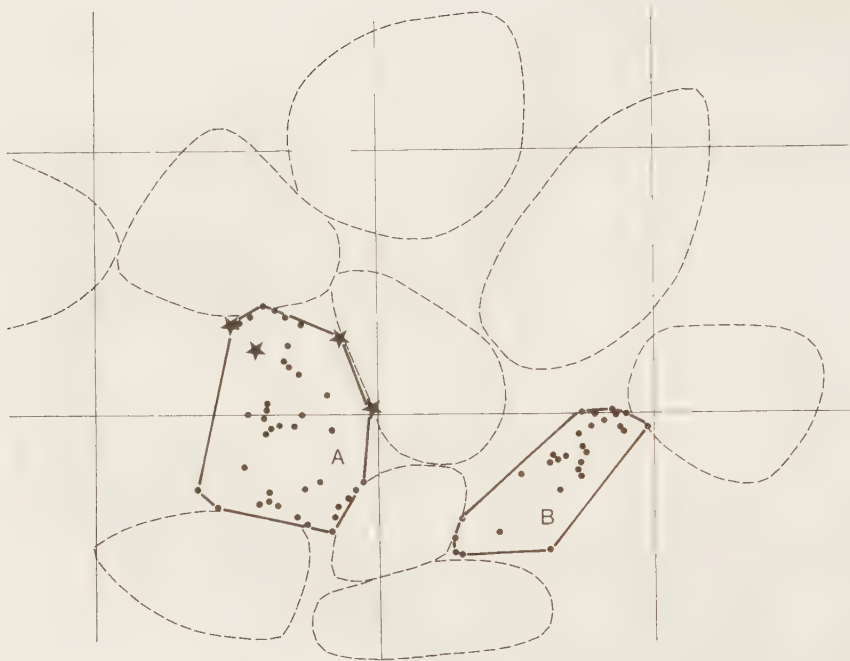


Fig.3. Winter ranges during one season for two Common Buzzard pairs (A and B) with different perch sites marked. Stars denote places of territory defence. Neighbouring territories are indicated by dashed lines. Each square represents one square kilometre, and the area is the same as for the summer situation (Fig.2).

3.3. RESIDENCY AND JUVENILE DISPERSAL

Territorial pairs were resident in the area the whole year. Most juveniles, however, probably spent their first winter away from their birthplace, as indicated by ringing recoveries (Fig 4). All young birds born in the area had disappeared by the end of November.

3.4. MORTALITY

The loss of territorial adults within six territories was assessed during six years. Eight birds disappeared, six males and two females, and at least in three cases, probably in all, through mortality. This gives an annual mortality among adults of 11%, a low figure compared to those obtained from analyses of ringing recoveries (19% - Olsson 1958, 23% - Meunier 1961, 19% - Mebs 1964b).



Fig.4. Dispersal of juvenile Common Buzzards, ringed as nestlings in southern Sweden and recovered within their first year of life. The date 25.11 refers to a juvenile bird found dead in the study area.

4. REPRODUCTION

4.1. BREEDING PERFORMANCE

Out of 52 complete clutches, containing a total of 140 eggs, 42% consisted of two eggs, 46% of three eggs, and 12% of four eggs. Mean and median clutch size was 2.69 and 3, respectively. Mean number of fledglings was 2.09 and median 2.

The breeding performance was characterized by: (1) a high degree of hatchability (90%) with little variation between years (C.V.=8.9%), (2) a high (88%) and rather constant nestling survival (C.V.=12.1%), (3) a small variation between years in the number of fledglings per successful nest (C.V.=9.6%), and (4) a high proportion (83%) and small variation (C.V.=9.6%) in the number of incubated clutches that gave rise to fledglings (Tab 1). In contrast, the proportion of territorial pairs with fledglings varied substantially between years (C.V.=27.9%). Most of this variation was due to a considerable number of total failures before hatching (C.V.=20.5%). Whether these were related to an inability to lay eggs, as in the Sparrowhawk, *Accipiter nisus* (Newton 1976), or to incubate successfully, as in the Kestrel,

TABLE 1

Breeding performance in a Common Buzzard population studied during six years in southern Sweden. In 1975, the number of territorial pairs present was not sufficiently recorded. Hatching success includes only single losses, either added eggs or eggs disappeared for unknown reasons. The proportion of hatched eggs giving rise to fledglings includes only single losses since all losses of whole broods were due to accidents. The proportion of laid eggs producing fledglings, however, includes all sorts of losses. $\bar{n}$ denotes number of eggs or nestlings except for the column of mean clutch size.

Year	No. of territorial pairs studied	No. of pairs successfully incubating	Proportion of territorial pairs incubating successfully	Proportion of incubated clutches producing fledglings	Proportion of territorial pairs with fledglings	Mean clutch size	Proportion of eggs hatched	Proportion of hatched eggs giving rise to fledglings	Proportion of laid eggs producing fledglings	No. of fledglings per successful breeding pair	No. of fledglings per territorial pair
1975	(16)	16	-	88 %	-	2.75 (n=13)	83% (n=23)	89% (n=18)	54% (n=33)	1.78	-
1976	18	9	50 %	78 %	39 %	2.00 (n=5)	100% (n=10)	100% (n=10)	100% (n=10)	2.00	0.78
1977	17	11	65 %	73 %	47 %	2.80 (n=6)	82% (n=11)	100% (n=9)	78% (n=14)	2.25	1.06
1978	18	15	83 %	80 %	67 %	2.80 (n=10)	86% (n=22)	100% (n=18)	68% (n=28)	2.33	1.56
1979	21	18	86 %	94 %	81 %	2.83 (n=12)	97% (n=31)	81% (n=32)	79% (n=34)	2.18	1.76
1980	16	13	81 %	85 %	69 %	2.67 (n=6)	94% (n=16)	76% (n=17)	81% (n=16)	2.00	1.38
Total	90(106)	66(82)	73 %	83 %	61 %	2.69 (n=52)	90% (n=113)	88% (n=104)	72% (n=135)	2.09	1.37
Mean			73±15	83±8	61±17	2.64±0.32	90 ± 8	91 ± 11	77 ± 15	2.09±0.20	1.31±0.39
S.D.											
C.V.			20.5 %	9.6 %	27.9 %	12.1 %	8.9 %	12.1 %	19.5 %	9.6 %	29.9 %

TABLE 2

Breeding success and average egg weight in relation to clutch and brood size among Common Buzzards in southern Sweden.

	Clutch/Brood size		
	2	3	4
Proportion of eggs lost during incubation	12 % (n=40)	10 % (n=48)	4 % (n=24)
Proportion of young lost in the nest	15 % (n=40)	6 % (n=33)	0 % (n=20)
Proportion of eggs giving rise to fledglings	78 % (n=40)	67 % (n=69)	92 % (n=24)
No. of fledglings per nest	1.55 $\pm$ 0.76 (n=20)	2.04 $\pm$ 0.98 (n=23)	3.67 $\pm$ 0.82 (n=6)
Mean egg weight (g)	67 $\pm$ 7 (n=19)	61 $\pm$ 5 (n=25)	58 $\pm$ 2 (n=8)

Falco tinnunculus (Cavé 1968), could not be determined in this study due to a relatively low frequency of visits early in the breeding season. Out of 19 eggs lost, 12 were due to the loss of complete clutches, but these losses refer to clutches found relatively late in the incubation period. Among 11 young lost during the nestling stage, 6 were lost with whole broods, which were all blown down by strong gales. Thus the results strongly indicate that the time of egg laying and early incubation is a critical period for breeding buzzards.

4.2. OFFSPRING PRODUCTION IN RELATION TO CLUTCH SIZE, BROOD SIZE AND EGG WEIGHT

No significant differences in the proportion of losses at the egg or nestling stage were found when comparing clutches of two, three or four eggs (Tab 2). Eggs from clutches of four, although few, gave rise to a significantly higher proportion of fledglings than both clutches of two (by numbers, $\chi^2 = 4.30$, $p < 0.05$) and three eggs (by numbers, $\chi^2 = 4.47$, $p < 0.05$). Clutches of four eggs produced significantly more fledglings than clutches of both two ($t = 5.89$, $df = 24$, $p < 0.001$, one-tailed) and three eggs ($t = 3.73$, $df = 27$, $p < 0.001$, one-tailed), clutches of three eggs producing more young than those of two ($t = 1.83$, $df = 41$, $p < 0.05$, one-tailed).

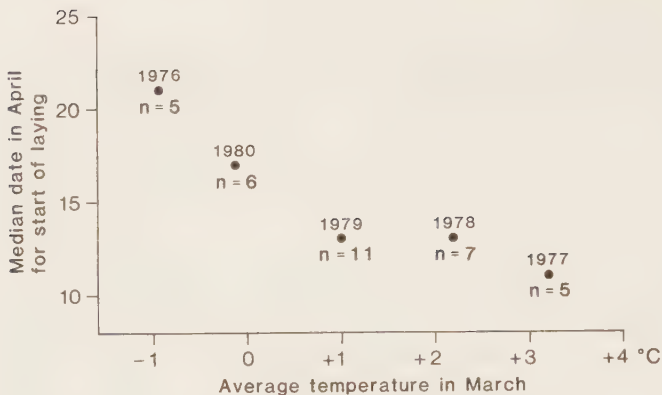


Fig.5. Temperature influence upon the start of egg laying in Common Buzzards in southern Sweden ($r = 0.83$, $t = 2.59$, $p < 0.05$, one-tailed; $r_s = 0.98$, $p < 0.05$).

The mortality among fledglings from the time of nest departure to near independence from the parents seems to be negligible. In 1978 and 1979, 34 young belonging to 14 broods (3 broods of one, 4 broods of two, 5 broods of three, and 2 broods of four young) were monitored. From early July to late August not a single loss occurred. Regardless of brood size, the parents obviously had no difficulty in providing their young with adequate amounts of food.

Eggs from clutches of two weighed significantly more than eggs from clutches of three ($t = 2.98$, $df = 42$, $p < 0.01$, one tailed) and four ($t = 3.37$, $df = 25$, $p < 0.01$, one-tailed). No statistically significant differences were found in average egg weight between clutches of three and four ($t = 1.59$, $df = 31$, $p > 0.05$). Apparently, egg weight had no significant influence on productivity; neither did it affect hatchability nor nestling survival.

4.3 TIME OF LAYING

4.3.1. INFLUENCE OF FOOD SUPPLY AND SPRING TEMPERATURE

In spring, Field Voles is the most prominent prey category for the buzzards constituting 48% in March and 32% in April of the prey biomass (Sylvén, in prep.). Since the Field Vole showed no statistically significant variations in spring density within the study area during 1975-79 (Hansson 1980, Nilsson 1981), the influence of food availability on timing is uncertain. Other im-

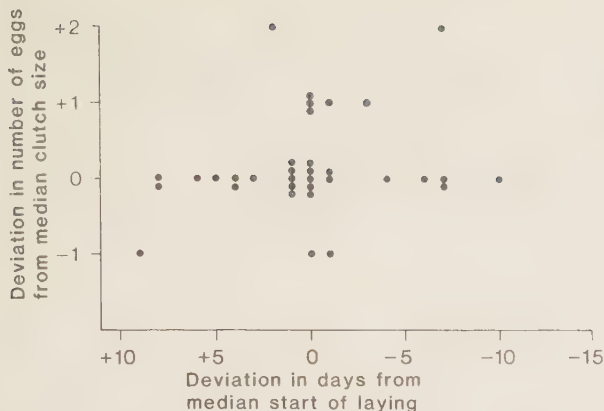


Fig.6.Clutch size in Common Buzzards in relation to the start of laying in the same year ($r=0.24$, $t=1.40$, $df=32$, $p>0.10$, two-tailed).

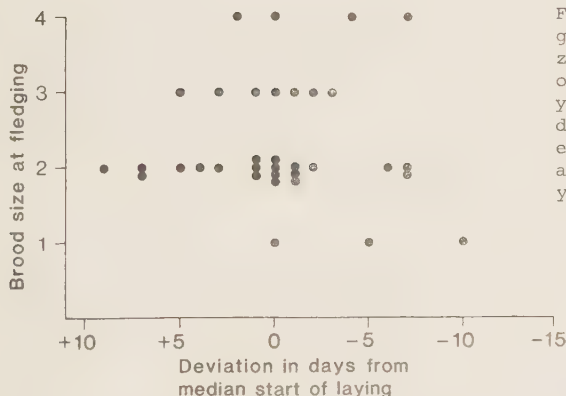


Fig.7.Brood size at fledging time in Common Buzzards in relation to start of egg laying in the same year ($r=0.02$, $t=0.14$, $df=32$, $p>0.8$, two-tailed). Median brood size in all years consisted of two young

portant prey categories at this time of the year are Water Voles, Moles, Talpa europaea, and, in April, frogs, Rana spp. (Sylvén 1982c), but no information is available about variations in the abundance of these species.

The start of egg laying was significantly related to spring temperature (Fig 5), a decrease in mean March temperature of 1°C postponing laying by about two days.

4.3.2. INFLUENCE OF LAYING TIME ON CLUTCH AND BROOD SIZE

Within each year, the influence of laying date seems to be insignificant, both with regard to clutch size (Fig 6) and brood size at the time of fledging (Fig 7). The time of laying and the cor-

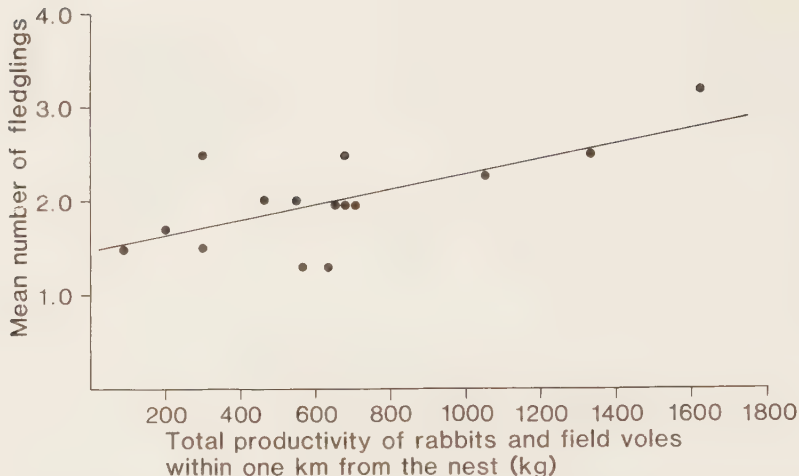


Fig.8. Relationship between breeding output in Common Buzzards and the local productivity of Rabbits and Field Voles with body weights of 0.20 and 0.03 kg, respectively ($r = 0.68$, $t = 3.31$, $df = 13$, $p < 0.01$, two-tailed; $r_s = 0.59$, $p < 0.05$).

responding clutch size of four different females, checked during at least three years, confirm this view (Tab 3).

4.4. INFLUENCE OF LOCAL FOOD SUPPLY

The average number of fledglings was positively related to the production of Rabbits and Field Voles within one kilometre of each nest (Fig 8).

4.5 INFLUENCE OF PREY CHOICE ON NESTLING SURVIVAL

The diversity of the prey brought to the nests increased significantly with decreasing Rabbit abundance ($r = -0.81$, $t = 2.40$, $df = 3$, $p < 0.05$, one-tailed), but this variation had no apparent influence upon nestling survival in different years (Tab 4).

5. DISCUSSION

5.1. TIMING

5.1.1. THE PROXIMATE CONTROL

The immediate factor influencing the start of breeding in many birds is the female's ability to obtain enough food to form eggs (Perrins 1965, Lack 1966) and acquire enough body reserves to endure the incubation period (Newton 1979). A substantial amount of evidence, both circumstantial and experimental, has accumulated in recent years in support of the view that the local food supply,

TABLE 3

Start of egg laying (date in April) and clutch size in four Common Buzzard territories in southern Sweden. The same females were involved in each territory while some changes of males occurred.

Year	Date of first egg and clutch size in territory			
	A	B	C	D
1	21 - 2 eggs	21 - 2 eggs	11 - 4 eggs	13 - 2 eggs
2	14 - 2 eggs	14 - 2 eggs	17 - 4 eggs	11 - 3 eggs
3	13 - 3 eggs	24 - 2 eggs	24 - 4 eggs	12 - 3 eggs
4	-	-	-	6 - 3 eggs

TABLE 4

Index of Rabbit abundance in spring (from von Schantz 1981), diversity of prey ("percentage similarity", Colwell & Futuyama 1971) brought to the nestlings, and nestling survival in six years of Common Buzzards breeding in southern Sweden. n denotes the number of prey items.

Year	Index of Rabbit abundance	Diversity of prey brought to the nests	Nestling survival in per cent
1975	200	1.64 (n=103)	89
1976	300	1.88 (n= 45)	100
1977	120	4.46 (n= 48)	100
1978	90	3.32 (n= 93)	100
1979	70	5.67 (n= 85)	81
1980	40	4.87 (n= 20)	76

working through the female, exercises the proximate control of the initiation of breeding (Drent & Daan 1980). Spring temperature and rodent density were found to influence the start of breeding of Kestrels in Holland (Cavé 1968, Drent & Daan 1980) and Tawny Owls in Great Britain (Southern 1970, Hirons 1976), and the influence of temperature was obvious also in the buzzard population examined in the present study.

TABLE 5

Estimated daily energy consumption of female Common Buzzards at different average temperatures in March. For information about the activity pattern and methods for calculation of energy costs, see Sylvén 1982 b.

	Proportion of day devoted to different activities	Estimated daily energy consumption (Kcal) at	
		-0.9°C	+3.2°C
Nightly resting	47.6 %	75	72
Daytime perching	45.7 %	72	69
Flapping flight	1.8 %	15	15
Soaring flight	4.9 %	12	12
Total		174	168

The buzzards delayed egg laying in response to low temperatures in March probably for two reasons: weather (1) influenced the availability of prey, and (2) affected the food needs of the birds themselves. The latter effect is probably quite important. Data about the activity pattern of Common Buzzards in March in southern Sweden and corresponding estimates of energy consumption (Tab 5) suggest a daily metabolic increase of 6 Kcal or 3.6% as a result of a decrease in average temperature of 4.1°C (the difference in mean temperature in March found for the period 1975-1980 in the study area). With an efficiency of 87% when utilizing fat reserves (Ricklefs 1974), this equals a decrease in body weight of 23 g during one month, corresponding to a decrease of about 40% in the general fat level of female Common Buzzards at this time of the year (Piechocki 1970). This indicates that even a small decrease in ambient temperature in the period before breeding starts can have important effects.

5.1.2. THE ULTIMATE BACKGROUND

The ultimate reason for the timing of breeding is to enable birds to raise young at the time of the year when food is most readily available. For bird-eating raptors in temperate areas, it is important to time the raising of nestlings to the mid-summer peak in prey abundance. In such species, the late nestling stage and

the time before the young become independent corresponds, however, to a time when the vulnerability of the prey is decreasing again (Snyder & Wiley 1976). A relatively high mortality towards the end of the breeding cycle has been demonstrated in several North American Accipiter hawks (Snyder & Wiley 1976). Raptors preying primarily on small and medium sized mammals generally face a different food situation during the breeding season compared to bird-eaters. Small mammals increase from a low in spring to a peak in early autumn (Fig 9). Therefore, raptors feeding mainly on small mammals do not have to time the start of breeding very closely to any peak in prey abundance later in summer.

In many species, a seasonal decline in clutch size has been demonstrated (for a review, see Klomp 1970). This has been interpreted as an adaptation to reduced prey availability later in the season, reflected in a lower nestling survival. In Sparrowhawks, fewer nests produced young in the second half of the season than in the first (Newton 1976). An analysis of ringing recoveries of Dutch Kestrels revealed that late-fledged young had a higher mortality rate in late summer and early autumn than young raised earlier (Cavé 1968). However, Cavé (1968) presented no explanations for these findings. Ringing recoveries of Common Buzzards have not yet been analyzed from that aspect, but this study did neither reveal any seasonal decline in the number of young fledglings, nor any differences in post-fledging survival between broods of different sizes.

Both in Kestrels (Cavé 1968) and in Sparrowhawks (Newton 1976) part of the seasonal decline in clutch size was related to first-year birds laying later and producing smaller clutches. Early breeding Red-tailed Hawks, Buteo jamaicensis, and Red-shouldered Hawks, Buteo lineatus, also laid more eggs and produced more young than hawks starting late (Snyder & Wiley 1976). In the Red-shouldered Hawk, much of this variation was attributed primarily to variations in habitat quality. Pairs breeding in wet, wooded areas with a rich supply of perching sites started earlier, laid more eggs, and produced more fledglings than hawks occupying dry areas with fewer perching trees. Clutches of pairs breeding in good habitats did not differ in size whether being laid before or after median laying date. For Common Buzzards breeding in southern Sweden, a seasonal decline in clutch size was not shown, so selection for early breeding in order to increase reproduction in the same season seems unimportant.

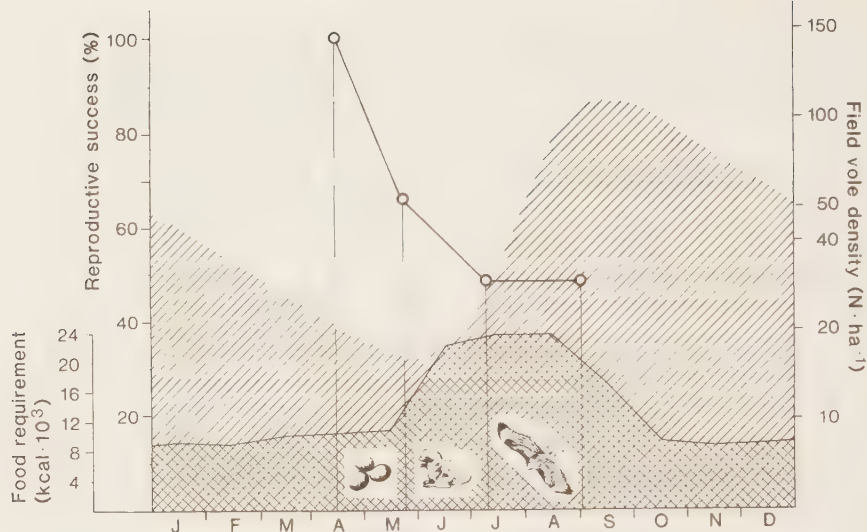


Fig.9. Estimated monthly food requirement in energy for a Common Buzzard pair in southern Sweden (cross-hatched area, from data in Sylvén, 1982 b) in relation to seasonal variations in Field Vole density in optimal habitats within the study area (striped area, from Erlinge et al. 1982). The reproductive success at different stages of breeding is expressed as the percentage number of hatched eggs and fledglings in relation to total number of laid eggs. Data are from Tab.1 assuming that those complete losses early in the season, where the reason for the failure was unrecorded, involve pairs laying the average clutch size found for the entire period but missing in early incubation.

Early breeding sometimes enables pairs to rear more than one brood per year. Apart from some tropical raptors (e.g. Pale Chanting Goshawk, *Melierax poliopterus*, Smeenk & Smeenk-Enserink 1975), this has been reported rather frequently in several rodent-eating species like the White-tailed Kite, *Elanus leucurus* (Pickwell 1930, Hawbecker 1940), Black-shouldered Kite, *E. caeruleus* (Tarboton, in Newton 1979), American Kestrel, *Falco sparverius* (Howell 1932, in Newton 1979), and Harri's Hawk, *Parabuteo unicinctus* (Mader 1975). Common to these species is that they are smaller than *Buteo buteo* and that their breeding cycles are shorter. The populations, from which these data come, also occupy areas with a subtropical or Mediterranean climate. But, as far as I know, the Common Buzzard seems to be entirely single-brooded within the whole of its breeding range.

The close timing of egg laying to spring temperatures strongly indicates that the buzzards start breeding as soon as the environmental conditions allow them to do so. They have this in common with a lot of other bird species (for a recent review, see Drent & Daan 1981). It has been suggested (Sylvén 1982b) that the ultimate reason for this early start is that it enables the buzzards to finish moult so early in autumn that they have time to accumulate sufficient fat reserves to survive the winter. A six-week delay of the start of breeding in order to adjust egg production to a period of more favourable food conditions would diminish total fat deposition in autumn by approximately 86% in males and by 73% in females. Since fat reserves are essential for winter survival, such a decrease would probably seriously jeopardize their life expectancy. Female Common Buzzards generally initiate moulting one month ahead of males (Sylvén 1982b). Provided they also finish moult correspondingly earlier they can also start putting on winter fat one month earlier than males; that they do so was supported by published information (Sylvén 1982b). The results therefore strongly indicate that the timing of breeding in the Common Buzzard has evolved to minimize moult stress on winter fattening in order to enhance survival and thereby lifetime reproduction.

5.1.3. CONSEQUENCES OF TIMING

Figure 9 shows the calculated energy expenses of a breeding pair of Common Buzzards during a year (Sylvén 1982b) in relation to density variations in one of the most important prey species, the Field Vole. Egg formation and incubation occurs at a stage of the vole cycle when the population is declining, mainly due to predation (Erlinge et al. 1982). The increase in food and energy demands due to the growth of nestlings coincides with a period of slow recovery of the vole population, while the post-fledging period takes place at a time when the vole population increases at its maximum rate.

Figure 9 also illustrates the loss rate at different stages of the breeding period. As can be seen, breeding performance seems to improve with season in spite of an increase in food requirement. I suggest the following explanations for this pattern.

In the pre-laying and laying period, female birds have to accumulate substantial amounts of body reserves to be able to breed. Protein is probably the most important material needed for egg formation and fat for incubation (Jones & Ward 1976, Newton

1979). To eliminate the considerable risk of destroying the developing eggs within the female body and to reduce the exposure of the eggs to predation, female Common Buzzards refrain from hunting during this period (Sylvén 1982c). Thereby the female misses all the energy she would otherwise have obtained from her own hunting efforts. The male buzzard provides all the food necessary to cover both her maintenance costs and those connected with egg formation. Although the daily energy expenditure of the male Common Buzzard peaks at this stage of the year (Sylvén 1982b), mainly due to a considerable hunting effort (Sylvén 1982c), the rate of prey delivery to the laying female was estimated just to cover calculated needs, leaving only narrow margins (Sylvén 1982c). The female probably has to base both egg laying and to some extent incubation on the energy provided by the male. In the Tawny Owl, accumulated fat reserves were found to be important for the female as a buffer against temporary inability of the male to provide food during incubation (Hirons 1976). Female Tawny Owls receiving inappropriate amounts of food during incubation were found to hunt on their own and many eggs chilled.

In this perspective, it is understandable why the early stages of reproduction is a difficult time for breeding buzzards. A pattern characterized by a substantial variation in total failures early in the season and a high hatchability and nestling survival if incubation was successful occurs in the Common Buzzard as well as in several other raptorial birds, e.g. Kestrels (Cavé 1968), Tawny Owls (Southern 1970), Sparrowhawks (Newton 1976), and Ural Owls (Lundberg 1981). In all these species, courtship feeding is well developed (see e.g. Tinbergen 1940, Lundberg 1980).

Although energetic costs of incubation probably are negligible in many species (see e.g. Walsberg & King 1978a,b), the fact that foraging time for one or both parents is more restricted at this stage than in any other period of the yearly cycle must be a factor of considerable importance (Yom-Tov & Hillborn 1981). One of few documented examples of the narrow food limits within which some bird species have to operate during incubation is the situation in the House Martin, Delichon urbica. Here the maximum amount of energy the adults can gather in the period available for foraging only exceeds the requirements by 6% (Bryant & Westerterp 1980). In this species, however, the eggs show a good ability to withstand chilling, especially in the early developmental stages, which allows the adults to maintain body condition at the small

cost of lengthening the incubation period.

For breeding Kestrels in Holland, clutch desertion was often correlated with variations in local food supply (Cavé 1968). In the Kestrel, as in the Common Buzzard, the male alone is responsible for the hunting during the incubation. If the male is unable to provide the female with adequate amounts of food and if her body reserves do not allow her to continue incubating without hunting for herself, the open-nesting habit of the Common Buzzard at least makes the clutch more prone to predation.

The nestling period seems to be a rather easy task for breeding buzzards in spite of a rapid increase in food requirements. Nestling survival was constantly high and a low proportion of the clutches that hatched was lost at this stage. During the first two years, Rabbits dominated the prey brought to the nestlings. But during a succession of unfavourable winters, the Rabbit population declined. This variation in food supply, with corresponding changes in the diversity of prey brought to the nestlings, did not have any apparent influence on nestling survival. A similar resistance to variations in the most important prey species was reported for breeding Kestrels in Holland (Cavé 1968). Although the density of Common Voles, Microtus arvalis, varied with a factor of about 50, survival rate was constantly high. In this species, as in the Common Buzzard, alternative prey species helped the birds to buffer against periods of low density of the most preferred food.

Young Common Buzzards survived the post-fledging period extremely well, something they have in common with several other rodent-eating raptors. Only 4 out of 231 Tawny Owls disappeared during the three months between leaving the nest and independence (Southern 1970), and in a total of 156 broods of Red-shouldered and Red-tailed Hawks in North America, no single loss was recorded during the fledgling dependence period (Snyder & Wiley 1976). Due to the abundant food supply most rodent-eating raptors face at the end of reproduction (Fig 9), their fledglings obviously get a most favourable start in life. Young buteos have also been found to develop hunting skill rather quickly, already within the post-fledging period, in contrast to most accipiters (Snyder & Wiley, Newton 1979).

Although the timing of breeding in southern Sweden seems to be far from optimal with regard to the early stages, the lifetime reproductive output of a Common Buzzard is quite impressive. For

the average adult buzzard, whether male or female, the mean expectation of further life is 8.6 years (calculated by the formula $2-m/2m$, where m is the annual mortality as a fraction of unity). With a mean of 1.37 fledglings per breeding attempt during the period 1975-1980 (Tab 1), an average buzzard living in an average territory would produce about 12 fledglings. With a first year mortality of 57% and a second year mortality of 30% for Fennoscandian buzzards (Olsson 1958), four individuals would survive until the age of two, when probably most Common Buzzards are able to start breeding (Glutz et al. 1971).

5.2. THE DETERMINATION OF BREEDING SUCCESS

5.2.1. CLUTCH SIZE AND BREEDING OUTPUT

Lack (1947-48) claimed that if clutch size is adjusted to the maximum number of nestlings for which the parents can find enough food and if clutch size is to a large extent inherited, the most productive clutch size will, by natural selection, also be the commonest.

For Common Buzzards in southern Sweden, a positive relationship between clutch size and offspring production was found, i.e. those buzzards laying most eggs also being most productive. This has also been demonstrated for Common Buzzards in Scotland (Picozzi & Weir 1974), where clutches of two eggs on the average produced 1.82, clutches of three eggs 2.58, and clutches of four eggs 3.67 young. Mebs (1964a), working on Common Buzzards in Germany, also found that clutches of four eggs resulted in more young than did clutches of two and three eggs. The differences were, however, not so large due to a higher nestling mortality in clutches of four (36%) than in the smaller ones (24%). A positive relation between the number of eggs laid and the number of young produced was also found in Kestrels in Holland (Cavé 1968). Since, in Common Buzzards, post-fledging survival until near independence was independent of brood size in southern Sweden, the number of fullgrown young at fledging reflects productivity.

The commonest clutch size of Common Buzzards in southern Sweden as well as in Scotland was three eggs, so both in this species and in the Kestrel (Cavé 1968), the commonest clutch size did not correspond with the most productive, as was postulated by Lack.

5.2.2. THE DETERMINATION OF CLUTCH SIZE

Lack assumed that clutch size has been adapted to correspond with the largest number of young that parents can feed. Judging from

the seasonal variations in energy expenditure of male and female Common Buzzards in southern Sweden (Sylvén 1982b), raising young does not necessarily involve a serious amount of work. The activity costs of the male, who bears the major expenses for breeding, actually reach their lowest values during the nestling period, despite the fact that he has to collect more food at this season than in any other period of the year. These results find some support in a brood-manipulation experiment reported by Picozzi & Weir (1974). In a Scottish Common Buzzard population, living largely on Rabbits like the ones I studied, they transferred two eggs from a clutch of four to a new nest already containing three eggs. All five eggs hatched, and all young fledged without any signs of undernourishment. This strongly indicates that many buzzards do not have to maximize foraging efforts when raising young. Both sexes are even able to spend a substantial amount of energy on moulting in this period (Sylvén 1982b). Evidently there is little indication that the clutch size in these Common Buzzard populations is adjusted to the maximum number of nestlings for which the parents can find enough food. However, we must not forget that the food situation both in southern Sweden and in Scotland may be exceptional. The buzzards base a substantial part of egg formation on rodents (Sylvén 1982c), while they raise their young mainly on Rabbits and birds. There is no reason to believe that the food situation in spring predicts the amount of prey available later during the nestling stage. It is therefore possible that the buzzards, due to the exceptional food situation, are not able to realize maximum breeding potential. But even so, Common Buzzards obviously have a good ability to deal with changing food conditions, such as when one of their basic resources (Rabbits) decline drastically.

As territorial boundaries tended to be stable from year to year, it is interesting to note the rather stable clutch size found in several territories (Tab 4). But since the same females occupied these territories (while some changes of males occurred), it is unclear if this stability was associated with the quality of the territory or to the fitness of individual birds. However, the local abundance of Rabbits and voles influenced the production of offsprings in southern Sweden (Fig 8). My data were insufficient to demonstrate a similar relationship between clutch size and food abundance, but since clutch size and breeding success were highly correlated, there is a strong indication that the number of

eggs laid by each pair was related to the quality of their territory. This agrees with results in other territorial species. In Magpies, Pica pica, about 86% of the within-year variance in clutch size was linked to differences in territory quality (Högstedt 1981).

An association between the production of offspring and different environmental features has also been established for several other raptor populations. For breeding Common Buzzards in Scotland (Picozzi & Weir 1974), the mean number of fledglings increased significantly with both increasing proportion and extent of farmland, and for the closely related Red-tailed Hawk in North America, productivity was positively related to the amount of fallow pasture within a radius of 1.2 km from the nests (Howell et al. 1978). In both these studies, the amount of habitat features was supposed to be indicative of prey abundance, although this relationship was never demonstrated. A correlation between the number of young produced and differences in the local food supply of different pairs was also established in Common Buzzards relying on Rabbits (Dare 1961, in Newton 1979), Black Eagles Aquila verreauxii, living on hyraxes (Gargett 1977), and Sparrowhawks living on songbirds (Newton 1976).

To summarize, the clutch size in the Common Buzzard seems to be related to the abundance of prey in each territory. To avoid jeopardising winter survival, the buzzards start breeding at a time of the year when food availability is limited. To prevent predation on the eggs and to eliminate the risk of destroying the eggs within the female's body, the female refrains from hunting and the male buzzard supplies her with most of the food she needs, not only for egg production but also for her maintenance. This exposes the buzzards to a considerable risk of failure early in the breeding season. But once beyond this critical period, they have no difficulties in raising young, and the juveniles fledge at a time of the year when the food situation continues to be favourable for several weeks.

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SEASONAL ALLOCATION OF ENERGY EXPENSES FOR ACTIVITY, REPRODUCTION
AND MOULT IN RELATION TO SURVIVAL IN COMMON BUZZARDS Buteo buteo.

ABSTRACT

Seasonal variations in activity and corresponding energy expenditures were examined in a sedentary population of the Common Buzzard, Buteo buteo, in southern Sweden. Males reached their highest levels in the early part of the breeding season when feeding their mates. In spite of high expenses when feeding nestlings, this period did not involve a serious level of work. The most demanding period during the year, when the buzzards have to maximize food intake per time available for feeding, occurs in mid-winter due to few hours of daylight. This period coincides with a peak in mortality. Timing of egg laying and breeding probably has evolved to minimize the impact of moulting on winter fattening in order to enhance survival and thereby lifetime reproduction. Earlier moulting in females compared to males could be a contributory factor behind a higher survival rate in females than in males.

The adaptive background of the seasonal allocation of resources to different demanding activities such as breeding, moult and migration in relation to environmental conditions is of considerable interest when evaluating different life patterns in animals. Two limiting resources, interrelated in a complex way, are time and energy (King 1974). Natural selection probably operates in such a way as to optimize the allocation of these two resources to self-maintenance and reproduction. The annual pattern of the interaction of these two basic resources has, however, only been elucidated in a few bird species (for a review, see Walsberg 1980).

The aim of this paper is to present the daily time and corresponding energy budgets of adult Common Buzzards, Buteo buteo, throughout the year in southern Sweden. The study is based on two years' data collected during a rather favourable food situation. On this basis I will try to illustrate in particular some aspects of the intricate problems related to breeding and moult and how these demanding and interacting activities are arranged in order to optimize the lifetime reproductive output.

The analysis is based on a conversion of different activities into energy units based on laboratory measurements and the application of these figures to field conditions. I am fully aware of all the shortcomings of such an attempt. The main interest, however, is not to obtain absolute figures but to get a satisfactory picture of the relative costs of different activities. The Common Buzzard is a rather suitable study candidate due to its almost

phlegmatic habits, easy both to classify and quantify, and also because, like some of its close relatives, it has been the subject of several physiological studies relevant to this kind of analysis. Also, the activities of the Common Buzzard are almost entirely limited to a well-defined territory, and hunting is mainly restricted to open country where the buzzards often use exposed perching sites.

STUDY AREA AND METHODS

The study was performed in southern Sweden (55.42°N , 13.25°E) within an area previously described in several papers (see e.g. Sylvén 1978). In 1975-1976, the daily activity of adult, territorial buzzards was assessed during observation periods of approximately four hours, randomly distributed within the daily activity period (approximately half an hour before sunrise to half an hour after sunset) and between days. Three different activity levels were distinguished: perching, soaring, and flapping flight. Since flight activity within the diel cycle peaks around noon irrespective of season (for the winter period, see Sylvén 1978), total daily activity was assessed after first evaluating the activity pattern within each hour of the day separately and then summing the total time devoted to each of the three activities.

The time budget is based totally on approximately 340 hrs of field notes. For the winter period (October - March), the material from either sex has been combined with data from unspecified buzzards to obtain a satisfying level of information. This material is assumed to reflect the activity pattern in both males and females. The allocation of the study effort (Tab 1) reveals a dominance in time devoted to the breeding season, especially its earliest part (April).

Temperatures are monthly means at Lund (approximately 20 km west of the study area) from the period 1931-1960 reported by the Swedish Meteorological and Hydrological Institute except for April, where the average temperatures on a five day basis refer to the period 1975-1980. To relate temperatures to different stages of the breeding cycle, the median date for start of laying in 1975-1980, i.e. 15 April, was used as a reference.

Several studies of raptors have revealed a rather close agreement between the energy consumption estimated from time budget studies and that based on observed food consumption (Tarboton 1978, Wakeley 1978, Koplin et al. 1980). A slightly modified mo-

TABLE 1

Amount of registered monthly activity in minutes among Common Buzzards studied in southern Sweden in 1975-1976. Data in May were collected in the second half of the month corresponding to the end of incubation and early nestling period. In June, the activity was examined during the second half of the month at the end of the nestling phase.

Months	Males	Females	Unspecified sex	Total
Jan	-	22	498	520
Feb	-	26	307	333
Mar	-	165	686	851
Apr	5343	4582	-	9925
May	565	670	-	1235
Jun	1785	1557	-	3342
Jul	556	421	-	977
Aug	395	205	-	600
Sep	670	438	-	1108
Oct	123	384	182	689
Nov	34	71	523	628
Dec	-	-	218	218
Total	9471	8541	2414	20426

del of Koplin et al. (1980), supplemented with terms describing the energy costs of breeding and moult, was used in this study to estimate the daily energy expenditure (DEE) of the buzzards:

$$DEE = EM_{T_a} + P_{Ff} (BMR) (FC) + P_{Sf} (BMR) (SC) + E_M + E_{Egg}$$

where: EM_{T_a} = existence metabolism at the appropriate season with an ambient temperature of T_a

BMR = basal metabolic rate

P_{Ff} and P_{Sf} = duration of flapping flight (Ff) and soaring flight (Sf) as a proportion of the day (24 hrs)

FC and SC = coefficients of flapping (FC) and soaring flight (SC) in relation to BMR

E_M = energy cost of moult

E_{Egg} = energy cost of egg formation

TABLE 2

Weight changes during winter of Common Buzzards in southern Sweden and Central Germany. The material from Sweden is based on 111 live-trapped birds while the German material consists of dead specimens analyzed by Piechocki (1970). Weights of both sexes are combined.

Month	Mean body weight (g)	
	Central Germany	South Sweden
December	992 (n=31)	989 (n=27, s.d.=125)
January	922 (n=48)	964 (n=27, s.d.=163)
February	882 (n=82)	928 (n=39, s.d.=123)
March	862 (n=34)	906 (n=16, s.d.=104)

By using this model, I have adopted the view of Kendeigh et al. (1977) that the energy cost of flight should be added to the existence metabolism to obtain the total energy expenditure for a period. This because the energy saved in temperature regulation during flight is more than offset by the extra feeding activity required to replace the energy used in flight.

How the different costs were estimated is presented in detail in the following section together with the methods used to determine some additional expenditures connected with breeding which are excluded from the general model for reasons given below.

An important part of the analysis deals with the interrelation between the calculated seasonal change of energy expenditure and variations in body weight due to the deposition or using up of fat stores. Although I did not study fat deposition, details are available from Central Germany (Piechocki 1970). The buzzards in both areas experience very similar conditions, both with regard to climate and vegetation, and exhibit almost identical population dynamics (compare Mebs 1964a,b with Sylvén, this thesis). I therefore assume that the pattern of fat deposition among adult Common Buzzards in Central Germany (Fig 1) reflects the situation in southern Sweden, especially as the weight changes found in winter are identical in the two populations (Tab 2).

ENERGY EXPENDITURE FOR SELF-MAINTENANCE

(1) BASAL METABOLIC RATE

Measurements of the basal metabolic rate (BMR) of two female and one young buzzard were reported by Jud & Kulzer (1975). Their

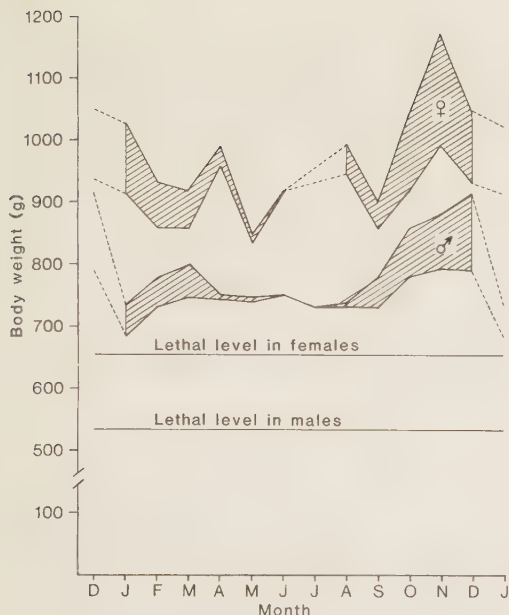


Fig.1. Variation in fat deposits (shaded areas) and body weight in male and female Common Buzzards (compiled from data in Piechocki 1970).

average value (Tab 3) is 103% of the rate predicted by the non-passerine equation of Lasiewski & Dawson (1967) and 85% of the rate predicted for a 1.06 kg falconiform by the equation of Zar (1968). No measurements exist on males, but using the regression line for non-passerines of Lasiewski & Dawson (1967) for a male buzzard, with the average weight of 0.79 kg (Piechocki 1970), yields a figure amounting to 81% of the female's BMR in absolute terms and to 108% on per weight unit basis (Tab 3).

Diel variations in body temperature were reported by Jud & Kulzer (1975), with 40.4°C during the day and 38.5°C during the night. If this corresponds to a daily rhythm in BMR, as reported for many birds by Aschoff & Pohl (1970), is unknown. Since a seasonal variation in BMR is most noticeable in small birds (Weathers 1980), the difference in BMR between summer and winter acclimatized buzzards is regarded as negligible.

(2) TEMPERATURE REGULATION

Data on the temperature dependent oxygen consumption below the thermoneutral zone ($15\text{--}29^{\circ}\text{C}$) in three captive, summer acclimatized female buzzards (mean weight 1.01 kg) were reported by Jud & Kulzer (1975). A linear regression of their measured values at 0, 5, 10, and 15°C demonstrated a relationship between metabolism

TABLE 3

Basal metabolic rate (BMR) of male and female Common Buzzards. The figure for females is based on measurements of two adult individuals (Jud & Kulzer 1975) whereas the male value is estimated from the equation given by Lasiewski & Dawson (1967).

Sex	Body weight (kg)	BMR (Kcal/day)	BMR per weight unit (Kcal/day, Kg)
Male	0.79	64	81
Female	1.06	79	75

(M) and ambient temperature (T_a): $M = 145 - 4.55 T_a$ ($r = 0.82$, $t=4.00$, $df=12$, $p < 0.001$). The temperature coefficient is 34% higher and the metabolism at 0°C is 7% higher than the predicted values (according to Kendeigh et al. 1977). Due to better plumage and fat insulation in winter, temperature regulation in most birds is then relatively less energy demanding than in summer. By using Kendeigh et al. (1977) formula for the metabolism at 0°C and for the temperature coefficient in winter acclimatized non-passerine birds and assuming that the difference between predicted and measured values found in summer birds also is applicable to the winter situation, the above temperature dependent relationship was transformed into a winter form (Tab 4).

For the smaller males, temperature regulation will be less demanding in absolute terms. The equations relating the energy consumption in summer and winter acclimatized male buzzards at different temperatures below the thermoneutral zone are given in Table 4, assuming the same relative increase of the temperature coefficient and metabolism at 0°C between predicted (according to Kendeigh et al. 1977) and "observed" figures as was found for females.

The temperature effect is, however, under the influence of solar radiation and convective heat transfer by the wind. Fortunately, the combined effect of these physical influences upon the temperature related metabolism has been evaluated in raptors of different sizes (Hayes & Gessaman 1980). For two Red-tailed Hawks, *Buteo jamaicensis*, weighing approximately as much as a female Common Buzzard in winter, the detrimental influence of wind upon metabolism was found to be slight, especially compared to the effects on five individuals of the much smaller American

TABLE 4

The post-absorptive metabolism (M) below the thermoneutral zone and the existence metabolism (EM) in relation to ambient temperature (T_a) in summer and winter acclimatized male and female Common Buzzards. The summer period coincides with moulting in both sexes.

	Summer	Winter
Males	$M = 119 - 3.97 T_a$	$M = 82 - 2.81 T_a$
	$EM = 142 - 1.59 T_a$	$EM = 129 - 1.41 T_a$
Females	$M = 145 - 4.55 T_a$	$M = 100 - 3.22 T_a$
	$EM = 160 - 1.69 T_a$	$EM = 146 - 1.52 T_a$

Kestrel, *Falco sparverius*. The hawks were not appreciably stressed, not even during the most severe conditions of the study with an ambient temperature of -17°C , zero radiation, and a wind speed of 13 m/s. The maximum reducing power of radiation on the metabolism, when the hawks were exposed to an insolation equivalent to clear-solar noon, amounted to 30%.

Birds, however, usually react to thermal stress conditions by behavioural responses (Calder & King 1974). Thus, on cold and windy days Common Buzzards were found to select calm perching sites exposed to the sun (pers.obs.). The maximum reduction in metabolism due to solar radiation at noon for wintering Red-tailed Hawks perching under such circumstances was calculated by Hayes & Gessaman (1980) to be 8%. This estimate is probably applicable also to wintering Common Buzzards in southern Sweden. Due to such behavioural responses, it therefore seems justifiable to exclude the influences of both wind and radiation from the calculations.

(3) EXISTENCE METABOLISM

The energy metabolism of Common Buzzards engaged in nonflight activities both during day and night was estimated by the temperature dependent Existence metabolism (EM_{T_a}). This integrates basal metabolism, temperature regulation, ^a the heat increment of feeding associated with the digestion and assimilation of food, and the energy expended in a limited cage activity (Kendeigh et al. 1977). The temperature coefficient of existence metabolism is considerably lower than that of the temperature regulation in

a post-absorptive state mainly because EM_{T_a} includes the heat increment of feeding which can pay for an important part of the cost of thermoregulation at ambient temperatures below the lower critical temperature (Kendeigh et al. 1977). EM_{T_a} therefore is probably the most appropriate measure of the nonflight activity cost.

The existence metabolism of a Common Buzzard (weighing 0.98 kg and probably a female) was reported by Gavrilov & Dolnik in Kendeigh et al. (1977) as: $EM_{T_a} = 160 - 1.69 T_a$. This relation refers to the summer photoperiod. The measured values of existence metabolism at 0°C and of the temperature coefficient are 88 and 91%, respectively, of the predicted. Using these discrepancies and the regressions for the various parameters in non-passerines presented by Kendeigh et al. (1977), the relationship between EM and ambient temperature (T_a) for a male Common Buzzard (body weight 0.79 kg) is: $EM_{T_a} = 142 - 1.59 T_a$.

Due to improved insulation in winter, the effect of temperature upon EM is lessened. Using the linear regressions of EM at 0°C and of the temperature coefficient for the winter photoperiod given by Kendeigh et al. (1977) for non-passerines and assuming the same relative differences between predicted and "observed" figures as for the summer period, an estimate is made of the emperature dependent EM for both males and famles. The results are presented in Table 4.

(4) FLIGHT

Kendeigh et al. (1977) presented a regression of empirical values on the energy cost of active, flapping flight in relation to body weight for 11 non-passerine species. From this regression one finds that a Common Buzzard, weighing on average about 0.90 kg, will consume 36 Kcal per hour of active flight. This corresponds to a level 12 times BMR.

Gliding or soaring flight is, however, much less energy consuming than active flight (Pennycuick 1972, Kanwisher et al. 1978). Baudinette & Schmidt-Nielsen (1974), measuring the metabolic rate in two gliding Herring Gulls, Larus argentatus, found a rate between 3.2 and 4.1 times the level of BMR, and they concluded that gliding flight represents an increase of energy consumption to about twice the resting level (the resting level of the gulls in the experiment = $1.7 \times \text{BMR}$). Using a value for soaring or gliding flight of $3.4 \times \text{BMR}$, gives an energy consumption of about 10 Kcal per hour in the buzzards.

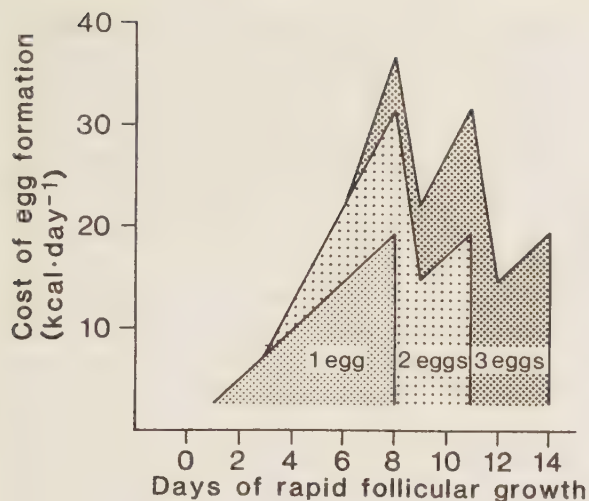


Fig.2. Calculated daily energy cost of egg production for a clutch of three eggs in the Common Buzzard (for details, see the text).

ENERGY EXPENDITURE OF BREEDING

(1) GONADAL GROWTH

Ricklefs (1974) estimated the cost of rapid gonad growth in males to be about 0.95% of BMR. In females, the energy requirements of ovary and oviduct growth also seem to be negligible, although slightly more costly than the corresponding gonadal growth in males (Ricklefs 1974). Both costs are ignored in this analysis.

(2) EGG PRODUCTION

Mean egg weight at the time of laying amounted to 63 g (S.D. = 6, $n=52$) in the study area (Sylvén, this thesis). With the aid of a regression on data compiled by King (1973), the duration of the rapid phase of growth of the ovarian follicles was calculated to be 8 days (days of rapid follicular growth = $2.87 + 2.62 \log \text{egg weight}$). Assuming a daily linear increase in volume of 2.8% of the ovum (based on Ricklefs (1974): daily increase = $2/n(n+1)$; n = length of the period of rapid follicular development), an energy content per egg of 66 Kcal (1.05 Kcal/g, including the white, Ricklefs 1974), a total cost of 88 Kcal of producing one egg with an energetic efficiency of 75% (Ricklefs 1974), and a laying interval of three days (Mebs (1964a) specifies an average of 2.5 days), gives a maximum daily impact on the female of 46% of her BMR when producing three eggs (Fig 2). This figure, how-

ever, is a slight underestimate since the albumen is not deposited until the yolk passes down the oviduct at the end of the egg development. According to Ricklefs (1974), the proportion of yolk and white in eggs of hawks and owls is similar to that in passerine eggs, and since the white contributes about 40% of the energy content of a passerine egg, the maximum impact on the female at the day of ovulation (the day before the egg is laid) is probably higher than that calculated above.

The total cost of producing three eggs, which is the median clutch size in the study area (Sylvén, this thesis), was estimated at 264 Kcal during 14 days of rapid development.

(3) INCUBATION

Kendeigh (1963) derived a formula for the rate of heat loss from eggs by which it is possible to indirectly estimate the energy required to maintain eggs within the normal range of incubation temperatures. The necessary heat requirement (M , Kcal/day) for a female buzzard incubating three eggs (mean egg weight 63 g) in relation to the nest temperature (T_{na}) would be: $M = 125 - 3.6 T_{na}$ (specific heat loss of the eggs = 0.8 cal/g °C, rate of cooling of the egg = 1.20 °C/hr, °C, egg temperature = 35°C, proportion of egg surface covered by the incubating bird = 0.18, nest attentiveness = 0.987). The proportion of time spent by female buzzards on nests was assessed during approximately 31 hrs of observation in daytime. This gave a figure of 98.1%. Assuming an attentiveness of 100% during the night, the total time the female sits on the nest in the middle of the incubation period becomes 98.7%. This high attentiveness reduces the additional cost of rewarming the eggs after periods of inattentiveness - a cost that has been found to increase the total expenditure of incubation considerably in several species (Kendeigh et al. 1977, Biebach 1979, Vleck 1981).

The nest temperature is of course under the influence of the ambient conditions, but these complex relationships have not been examined for open nesting species. Measurements of the influence of ambient temperature on the nest temperature in hole nesting species indicate, however, that T_a influences T_{na} with a factor less than one (Kendeigh 1963, Vleck 1981).

For three species belonging to the order Falconiformes (Accipiter brevipes, Falco tinnunculus, F. vespertinus) and breeding in nests similar to those of the Common Buzzard, the mean nest

temperature was found to be 34°C (Ponomareva 1972, according to Drent 1975). These measurements were, however, obtained in arid areas probably with more favourable temperature conditions than southern Sweden. But since buzzard nests usually are huge constructions of twigs with a well insulated nest cup lined with greenery, the nest temperatures in this species may be about the same as in the three smaller raptors. Assuming a nest temperature of 34°C and applying the formula by Kendeigh (1963), the metabolic heat production needed for incubating three buzzard eggs would amount to 3.6 Kcal per day, i.e. about 4.5% of the female's BMR.

Opinions differ, however, if birds actually need any extra heat production or not to perform incubation. King (1973) proposed that the energy normally expended by the adult for maintenance and thermoregulation could be channeled to the eggs without any extra cost. This view was to some degree opposed to by Kendeigh (1973) and Ricklefs (1974). Some recent measurements of the metabolic rate in incubating and non-incubating individuals of three passerine species under the same environmental conditions (Biebach 1979, Vleck 1981, Mertens 1980) clearly illustrate that incubation really adds a cost to the adult bird at temperatures below the thermoneutral zone (25-30% for Sturnus vulgaris, 20% for Poephila guttata, and "considerably" for Parus major). The energy cost of incubation in raptors has been assessed only for the American Kestrel (Gessaman & Findell 1979). Under the same environmental conditions, one incubating female had a metabolism about 45% greater than when not incubating, whereas another female (and a male) did not show increased metabolism due to incubation. However, all measurements for the three passerines, and for the kestrel refer to species with larger total clutch weights in relation to body weight than has the Common Buzzard. Since the energy required for incubation is directly proportional to clutch weight, the relative cost of incubation in the Common Buzzard is probably less than in the above species.

The brood patch allows a rapid transfer of heat to the eggs without increasing the general level of heat dissipation over the whole body (Ricklefs 1974). The size of the brood patch has not been assessed for the Common Buzzard. Let us assume it amounts to the same proportion of the total body surface as in Zonotrichia leucophrys, Agelaius phoeniceus, and Empidonax

traillii (Walsberg & King 1978a,b), three passerines with a clutch size similar to that of the Common Buzzard. In that case, approximately 12% or 9.5 Kcal per day of the heat normally produced within the thermoneutral zone can be channeled through the brood patch into the eggs, i.e. nearly three times larger than the calculated need. This would allow a temperature gradient between the eggs and the nest of 3°C. Even below the lower critical temperature (15°C in the Common Buzzard), the heat generated by the female in thermoregulation could probably completely substitute for the increasing demand of incubation because the temperature coefficient for the heat needed in warming the eggs (3.6) is similar to the temperature coefficient of the female's metabolism (3.2). An since incubation seems to constitute a constant fraction of the metabolic rate of a non-incubating bird under similar conditions below the lower critical temperature (Vleck 1981), the direct cost of incubation probably is negligible over the whole range of ambient temperatures encountered by the buzzards during the breeding season.

(4) BROODING

After three weeks, nestling Common Buzzards are able to thermoregulate fully by their own (Jud & Kulzer 1975). Until then, the female must brood the young in a similar way as when incubating the eggs. However, as the nestlings develop the ability to regulate their own body temperatures, they will gradually relieve the female by an amount corresponding to their own heat production (Kendeigh et al. 1977). Even at the end of the embryonic development, the heat requirement of incubation can be reduced considerably through the heat produced by the embryos (19-25% in Falco sparverius, Gessaman & Findell 1979, up to 75% in Larus argentatus, Drent 1970). Since the extra heat requirement of incubation in the Common Buzzard probably is negligible, brooding should be even less demanding.

(5) NESTLING GROWTH

The development of thermoregulation and corresponding metabolism in the Common Buzzard has been examined by Jud & Kulzer (1975) (Fig 3). The mode of development of the metabolic rate seems to be intermediate between the altricial and the precocial forms (according to Ricklefs 1974).

Besides the total heat production measured by the gas exchange,

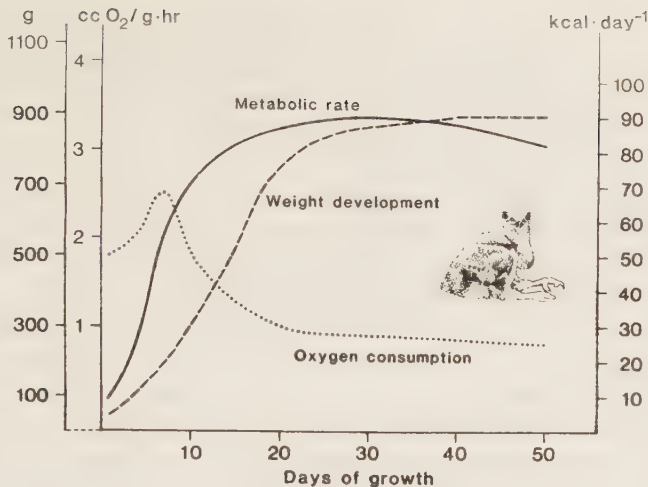


Fig.3. Weight development, oxygen consumption, and metabolic rate in a growing nestling of the Common Buzzard (compiled from data in Jud & Kulzer 1975). With a RQ of 0.80, 1 l oxygen is equivalent to 4.80 Kcal.

which includes both the cost of maintenance and biosynthesis, growing includes also an accumulation of energy in body tissues and some activity costs. The energy per gram body weight increases with age in most species, largely because the water content of tissues decreases but also because the content of lipids increases (Ricklefs 1974). I have not found any study on the variation in energy density in growing Common Buzzard nestlings or in any other raptor species, so to estimate roughly the gain in tissue energy with age in Common Buzzards, the energy density in White Leghorn chicks calculated by Ricklefs (1974) as 1.87 Kcal per gram wet weight has been used throughout the whole development of a buzzard nestling (Fig 4).

In growing Buteos, food consumption peaks around the fourth week of development (Olendorff 1974). Then the efficiency of weight gain, calculated as the increase of body weight per gram of food consumed, is about 25%. At this stage, Common Buzzard nestlings grow approximately 17 grams per day (Mebs 1964a, Jud & Kulzer 1975, pers.obs.). With the above density per gram wet weight and an energetic efficiency of about 75%, the cost of biosynthesis (about 12% of the metabolic rate) and corresponding tissue gain amounts to 42 Kcal per gram. The total energy meta-

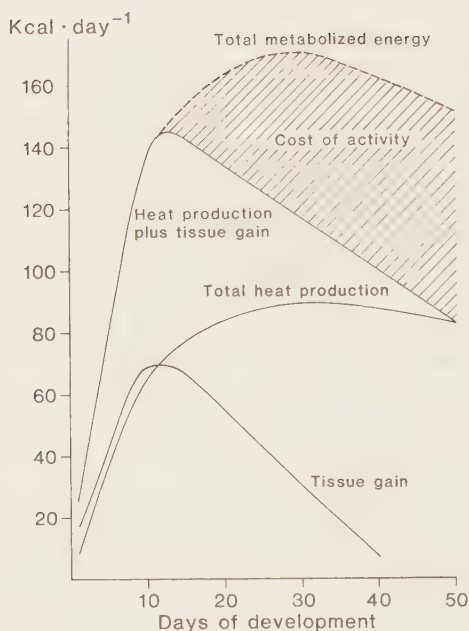


Fig.4. Estimated total metabolized energy of a growing Common Buzzard nestling and its different components (for details, see the text).

bolized at this stage could therefore be estimated at about 170 Kcal per nestling and day (42: 0.25), which corresponds to 1.9 times BMR. The difference between the metabolized energy and the heat production plus the tissue gain is supposed to constitute the cost of activity (Fig 4).

The total energy consumption per nestling during the first 50 days is estimated at about 7200 Kcal. This might, however, be an underestimate since the calculated energy metabolized at the midpoint of the linear growth period, approximately at the 15th day of development in Common Buzzards (Fig 3), only amounts to about 4.1 Kcal per gram weight increase. Drent & Daan (1980) report a very close value of 5.8 Kcal in eight species reviewed.

ENERGY EXPENDITURE OF MOULT

The knowledge of the physiological background of feather synthesis and of the corresponding energy costs is still impaired by a lot of uncertainties. In a recent review of the energetics of avian moult, King (1980) ends his account by suggesting that further studies be made, which hopefully can clarify some of the intricate questions connected with feather replacement in birds.

Two of the essential amino acids for the synthesis of feathers, cystine and cysteine, are much more concentrated in the feather protein keratin than in animal or plant proteins (Newton 1968). Moulting therefore probably involves an increase in food intake proportional to the difference in concentration of these amino acids in the plumage and in the food. Knowing the energetic costs of converting these compounds from the food into feathers, Kendeigh et al. (1977) presented a method by which the net energy cost of feather replacement can be estimated. They also found a good agreement between predicted costs and actual measurements of metabolizable energy intake in three passerine species.

This method assumes, however, that the animal does not synthesize cystine or cysteine from other amino acids - an assumption that is incorrect for at least some species (King 1980). If the energy cost of feather synthesis is additive to other maintenance needs of the animal is also uncertain. The assimilation of cystine and cysteine generates heat that can replace some of the extra heat requirement needed for temperature regulation in cold days (Kendeigh et al. 1977). However, some studies carried out to date indicate that the greater heat production during moult does not, or at least not wholly, cover the elevated thermostatic requirements of birds in moult (King 1980). So, in the absence of any measurements for Common Buzzards, I used the method proposed by Kendeigh et al. to estimate the energy cost of moult.

The net energy cost of converting the essential materials from the food into the feathers in carnivorous birds was estimated by Kendeigh et al. (1977) to be 57 Kcal per gram of feathers. With mean body weights of 0.79 and 0.99 kg of male and female Common Buzzards, respectively, plumage weights were determined using Turcek's (1966) equation. They were found to be 0.051 (male) and 0.063 kg (female). The total demand of moulting on male and female buzzards should therefore be 2907 Kcal for a male and 3591 Kcal for a female.

The Common Buzzard undergoes one complete moult annually (Cramp et al. 1980). Its duration is not satisfactorily documented, but the replacement of the primaries takes about five months (Bährman 1969). The moult starts with the body feathers followed by primaries, tail-feathers, and secondaries (Cramp et al. 1980). What proportion of the total plumage weight that is replaced at different stages of the cycle is, however, unknown. So, for the sake of simplicity, the daily impact of moult on the energy con-

TABLE 5

Initiation of moult on a monthly basis in female and male Common Buzzards breeding in southern Sweden. The figures show the percentage of birds with visible moult of primaries, secondaries, or tail feathers.

	Percentage of moulting birds	
	Females	Males
April	38 (n=13)	0 (n=12)
May	50 (n=38)	39 (n=31)
June	86 (n=29)	41 (n=27)
July	100 (n=30)	100 (n=16)
August	100 (n=29)	100 (n=23)

sumption is assumed to be evenly distributed over the whole moulting period (approximately five months). This gives a daily cost for moulting of 19 Kcal in males and 24 Kcal in females or about 30% of BMR in both sexes.

Female raptors usually initiate moult before the males (Stresemann & Stresemann 1960). According to the visible replacement of primaries, secondaries, and tail-feathers, some female buzzards in southern Sweden already begin moulting in April while the males wait until May (Tab 5). For this analysis, the modal female is supposed to start in May and the male in June.

VARIATIONS OF DEE WITHIN THE YEAR AND ITS GENERAL LEVEL

Based on time budget studies, the variation in daily energy expenditure was similar in males and females (Tab 6 & 7). Maximum DEE in males occurred in the pre-laying and laying period when they fed their mates (Fig 5), while females, much due to the cost of moulting, reached their highest level in June at the end of the nestling period when both parents provided food for their young (Fig 6). The generally high level of DEE in the nestling period is typical for at least some bird species (Walsberg 1980), but in breeding buzzards a considerable part of this high level was due to the cost of moulting (11% in males, 12-13% in females). Costs caused by activity reached their highest level in the early part of the breeding season, especially in males.

TABLE 6

Variation in daily energy expenditure (DEE) during different phases of the annual cycle in male Common buzzards in southern Sweden. Figures in brackets denote the percentage time of the day devoted to different activities.

Period	Mean ambient temp. (°C)	Average activity period (min)	Diurnal and nocturnal resting (Kcal)	Flapping flight (Kcal)	Soaring flight (Kcal)	Moult-ing (Kcal)	Total (Kcal)	Level of DEE in relation to BMR
JAN	-0.7	514	130 (98.4)	13 (1.5)	0 (0.1)	-	143	2.23
FEB	-0.8	634	130 (95.3)	10 (1.1)	8 (3.5)	-	148	2.31
MAR	1.3	763	127 (93.3)	15 (1.8)	12 (4.9)	-	154	2.40
APR, 1-5	3.9	851	124 (79.9)	19 (2.2)	43 (17.9)	-	186	2.90
" , 6-10	3.4	874	124 (81.0)	37 (4.3)	35 (14.6)	-	196	3.06
" , 11-15	5.2	897	122 (86.7)	33 (3.9)	22 (9.3)	-	177	2.76
" , 16-20	5.0	919	122 (86.6)	30 (3.5)	24 (9.9)	-	176	2.75
" , 21-25	6.8	941	119 (86.6)	25 (2.9)	25 (10.6)	-	169	2.64
" , 26-30	6.5	963	120 (86.2)	26 (3.0)	26 (10.8)	-	172	2.69
MAY	11.3	1030	113 (95.5)	7 (0.6)	10 (4.0)	-	130	2.03
JUN	15.2	1105	118 (93.4)	27 (3.1)	8 (3.5)	19	172	2.69
JUL	17.4	1074	114 (87.8)	14 (1.6)	25 (10.6)	19	172	2.69
AUG	16.8	962	115 (89.4)	13 (1.5)	22 (9.0)	19	169	2.64
SEP	13.5	824	121 (95.7)	8 (1.0)	8 (3.3)	19	156	2.44
OCT	8.7	687	128 (98.0)	6 (0.8)	3 (1.2)	19	156	2.44
NOV	4.8	555	122 (97.3)	14 (1.7)	2 (1.0)	-	138	2.16
DEC	1.9	539	126 (98.5)	11 (1.2)	0 (0.2)	-	137	2.14
Mean $\pm$ SD							154 $\pm$ 16	2.53 $\pm$ 0.07
C.V.							10.4 %	2.8 %

Males had lowest DEE values in May during the latter half of the incubation period, while a female minimum occurred in October. Maximum values equalled about 1.4 times minima in both males and females, i.e. slightly lower values than those (1.6) reported for *Pica pica* and *Phainopepla nitens* by Walsberg (1980).

In relation to BMR, males worked at a significantly higher level than did females (Tab 6 & 7, $t=4.84$, $df=32$, $p<0.001$, two-tailed). The average level of DEE, i.e. 154 Kcal in males and 168 Kcal in females (Tab 6 & 7), is accurately predicted by the general equation given by Walsberg (1980) on the relation between DEE and body weight in birds.

TABLE 7

Variation in daily energy expenditure (DEE) during different phases of the annual cycle in female Common buzzards in southern Sweden. Figures in brackets denote the percentage time of the day devoted to different activities. Mean ambient temperatures and the length of the activity period are the same as for the males.

Period	Diurnal and nocturnal resting (Kcal)	Flapping flight (Kcal)	Soaring flight (Kcal)	Egg production (Kcal)	Moulting (Kcal)	Total (Kcal)	Level of DEE in relation to BMR
JAN	147 (98.4)	13 (1.5)	0 (0.1)	-	-	160	2.02
FEB	147 (95.3)	10 (1.1)	8 (3.5)	-	-	165	2.09
MAR	144 (93.3)	15 (1.8)	12 (4.9)	-	-	171	2.16
APR, 1-5	140 (86.4)	15 (1.8)	28 (11.8)	-	-	183	2.32
" , 6-10	141 (91.4)	14 (1.6)	17 (7.0)	9	-	181	2.29
" , 11-15	138 (98.4)	4 (0.4)	3 (1.2)	27	-	172	2.18
" , 16-20	138 (98.8)	4 (0.4)	2 (0.8)	17	-	161	2.09
" , 21-25	136 (98.3)	3 (0.3)	3 (1.4)	-	-	142	1.80
" , 26-30	136 (98.3)	3 (0.3)	3 (1.4)	-	-	142	1.80
MAY	141 (99.5)	2 (0.2)	1 (0.3)	-	24	168	2.13
JUN	134 (93.0)	24 (2.8)	10 (4.2)	-	24	192	2.43
JUL	131 (93.3)	23 (2.6)	10 (4.0)	-	24	188	2.40
AUG	132 (94.9)	13 (1.5)	9 (3.6)	-	24	178	2.25
SEP	137 (94.9)	8 (0.9)	10 (4.2)	-	24	179	2.26
OCT	133 (98.0)	6 (0.8)	3 (1.2)	-	-	142	1.80
NOV	139 (97.3)	14 (1.7)	2 (0.1)	-	-	155	1.96
DEC	143 (98.5)	11 (1.2)	0 (0.2)	-	-	154	1.95
Mean $\pm$ SD						168 $\pm$ 14	2.11 $\pm$ 0.05
C.V.						8.3 %	2.4 %

Assuming that the fat levels given for male and female Common Buzzards by Piechocki (1970) reflect the situation in southern Sweden, a similar relation between daily energy expenditure and fat deposition on a monthly basis seems to exist in both sexes (Fig 7). During the summer period, with its generally high level of expenditure, the buzzards do not accumulate fat reserves, while in winter with low expenditures due to a limited activity, fat reserves are substantial. This pattern does not necessarily imply a stressed situation in summer time: during this period

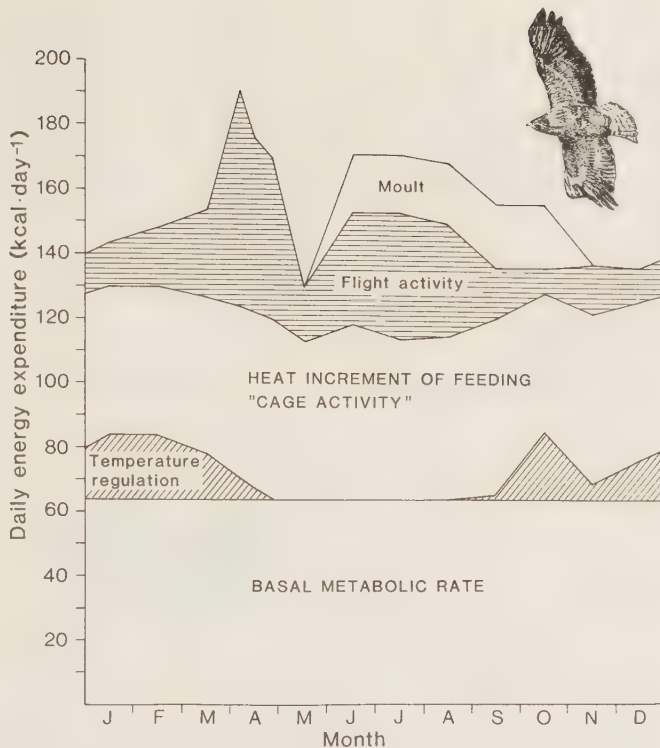


Fig.5. Daily energy expenditure on a yearly basis in male Common Buzzards in southern Sweden. Approximately 60% of the resting level was calculated to consist of basal metabolism and the cost of thermoregulation below the thermoneutral zone.

there is simply no need to buffer with fat against periods of food deprivation as there is in winter. It may even be a useful adaptation to reduce the load in order to minimize the costs of flight in connection with breeding duties (Freed 1981).

DEMANDING PERIODS WITHIN THE ANNUAL CYCLE.

To get a measure of the relative work level at different seasons, the daily energy expenditure was divided by the time available for feeding. Comparing this measure with the calculated need the bird has to collect food for in each period for self-maintenance, and in the breeding season for egg production, incubation, and nestling growth, gives an opportunity to identify demanding periods within the year (Tab 8).

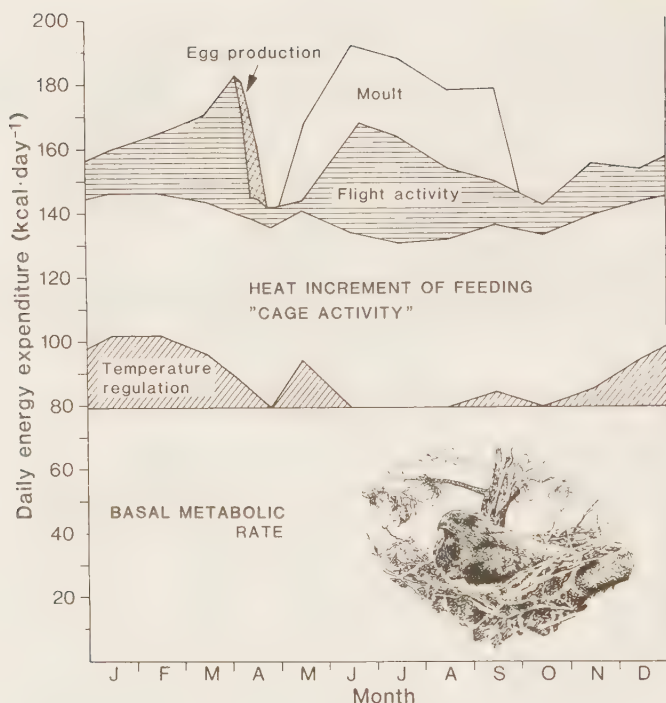


Fig.6. Daily energy expenditure on a yearly basis in female Common Buzzards in southern Sweden. Approximately 60% of the resting level was calculated to consist of basal metabolism and the cost of thermoregulation below the thermoneutral zone.

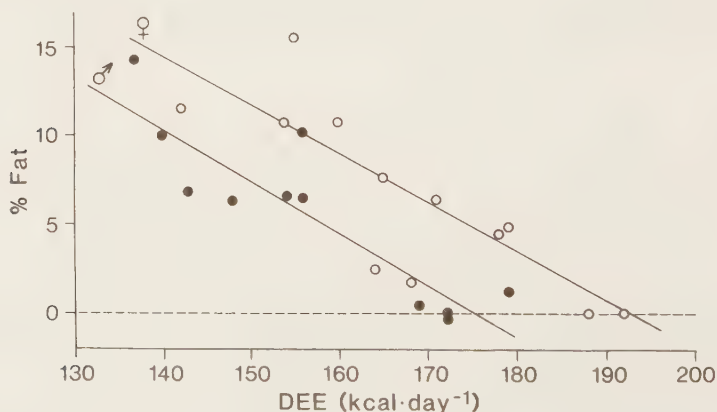


Fig.7. Percentage fat deposition in male (●) and female (○) Common Buzzards in relation to different levels of daily energy expenditure, DEE (for males: $r = 0.88$, $t = 5.73$, $p < 0.001$, two-tailed; for females: $r = 0.82$, $t = 4.51$, $p < 0.01$, two-tailed).

TABLE 8

The level of daily work in male and female Common buzzards, expressed as the daily energy expenditure (DEE) per hour activity, in relation to the energy each sex has to collect food for to cover their needs for self-maintenance and reproduction. The daily cost of growth and maintenance in two young buzzards (the median brood size in the study area, Sylven this thesis) was assumed to be covered mainly by the parents until the time of independence in the middle of September. The fledglings (one male and one female) were supposed to be as active as their parents. The energy cost to be covered by the female in June refers to the last half of the month.

PERIOD	M A L E S					F E M A L E S				
	DDE per hour activity (Kcal)	Energy cost to be covered (Kcal/hr)	Self-main-tenance (incl.moult) (Kcal/hr)	Feeding mate (Kcal/hr)	Feeding young (Kcal/hr)	DEE per hour activity (Kcal)	Energy cost to be covered (Kcal/hr)	Self-main-tenance (incl. moult and egg prod.) (Kcal/hr)	Feeding mate (Kcal/hr)	Feeding young (Kcal/hr)
JAN	16.7	16.7	16.7	-	-	18.7	18.7	18.7	-	-
FEB	14.0	14.0	14.0	-	-	15.6	15.6	15.6	-	-
MAR	12.1	12.1	12.1	-	-	13.4	13.4	13.4	-	-
APR	11.8	22.6	11.8	10.8	-	10.8	0	0	-	-
MAY	7.6	26.5	7.6	9.8	9.1	9.8	0	0	-	-
JUN	9.3	27.6	9.3	5.2	13.1	10.4	14.8	10.4	-	4.4
JUL	9.6	18.6	9.6	-	9.0	10.5	19.5	10.5	-	9.0
AUG	10.5	20.3	10.5	-	9.8	11.1	20.9	11.1	-	9.8
SEP	11.4	16.7	11.4	-	5.3	13.0	18.3	13.0	-	5.3
OCT	13.6	13.6	13.6	-	-	12.4	12.4	12.4	-	-
NOV	14.9	14.9	14.9	-	-	16.8	16.8	16.8	-	-
DEC	15.2	15.2	15.2	-	-	17.1	17.1	17.1	-	-



Fig.8. Within-year variation in the frequency of recoveries of adult Common Buzzards ringed in Germany (based on Mebs 1964b).

Outside the breeding season, January is the month when both male and female buzzards have to maximize foraging efficiency because of the limited amount of daylight available for hunting and because the costs of thermoregulation are maximal. The male is solely responsible for almost all hunting from the stage of egg formation until at least half the nestling period. Nevertheless, in spite of the great requirements, this seems to be a less demanding period than the rest of the year, probably due to favourable feeding conditions in late spring and summer. Apart from the period of parental duties, female buzzards experience the most favourable period in October.

THE SEASONALITY OF MORTALITY

Adult Common Buzzards in southern Sweden seem to survive very well. Based on a small sample, yearly survival was estimated at 89% (Sylvén, this thesis). The low mortality that occurred among territorial adults was confined to the winter period - a pattern in common with that in Germany (Fig 8); of 613 buzzards recovered dead at least one year after ringing, 61% were found in the period November to March (Mebs 1964b). Thus, the highest mortality coincides with the most demanding period during the year (Tab 8).

SURVIVAL AND SEX

In six breeding territories, studied during a six year period and where individuals were recognizable through wing tagging or plumage features, the female outlived the male in five territories. Out of 8 disappeared (at least three dead) birds, 6 were males and 2 females. Both female disappearances were recorded in the same territory, and all except one (a female) took place in the

TABLE 9

Starvation as a winter mortality factor in male and female Common Buzzards in Germany (compiled from Piechocki 1970). The proportion of starving birds is significantly higher in males than in females ($\chi^2 = 9.78$, $p < 0.01$, two-tailed).

	Males	Females
Starvation	110 (44%)	97 (30%)
Other death causes	142 (56%)	220 (70%)

winter period. These findings may be indicative of the generally higher death rate due to starvation among males than females found for German buzzards (Tab 9).

The different survival rates between the sexes are probably related to a difference both in the absolute and in the relative amount of fat and to a slightly different timing of fat deposition in male and female buzzards. This in turn, seems to be determined by the moult; females start moulting at least one month earlier than do males (Tab 5), and they probably also finish moult earlier. Thereby, females are able to use the longer activity period and higher ambient temperatures in October, compared to November for the males (see Tab 8), to start putting on winter fat - an interpretation that agrees with the results presented in Figure 1, based on data from Piechocki (1970).

Apart from the more favourable timing of fat deposition in females compared to males, females also accumulate both higher relative (♀: 15.6%, ♂: 14.2%) and absolute amounts of fat (♀: 183 g, ♂: 130 g) than do males. With maximum reserves and assuming an efficiency of about 87% when depleting fat and an energy value of 9.5 Kcal per gram fat (Ricklefs 1974), females are, on the average, able to withstand adverse conditions, e.g. snow cover, for 9 days with unaltered activity level (Tab 7) compared to 7 days for males. These periods are slightly shorter than those predicted from Calder's (1974) regression of observed survival times in various food-deprived birds against body weight (predicted values at ambient temperatures between -1 and -9°C : 12.3 days for females, 10.8 days for males). Birds exposed to food deprivation, however, often react by decreasing body temperature and metabolic rate (Koskimies 1950, Ivacic & Labisky

1973, Ketterson & King 1977, Shapiro & Weathers 1981). The decrease in BMR sometimes exceeds the predicted expected from the lowering of body temperature; this indicates also an active suppression of metabolism (Shapiro & Weathers 1981). These physiological responses could certainly increase the fasting ability of the buzzards to well above the calculated time. Piechocki's (1970) observations indicate that both male and female Common Buzzards do not die of starvation until falling to about 70% of their original weight (Fig 1) - an approximation also given for Falco sparverius by Shapiro & Weathers (1981). At this level the birds certainly have depleted protein reserves as well.

But, apart from the timing of fat deposition, the higher fat levels in females compared to males can also have another background. For both passerines and non-passerines, Calder (1974) presented allometric relationships between maximum fat deposition and body weight. Since fat reserves were found to increase faster in relation to body weight than corresponding energy expenditure, fasting endurance is probably better for large birds than for small, although their absolute consumption of energy still is higher (McNab 1971). But a priori, there is no obvious reason why fat reserves should be more favourable in large compared to small individuals of the same species. Since an important part of the fat accumulation in birds involves a subcutaneous deposition (Blem 1976), fat levels ought to increase in relation to body surface. The body surface (S , in cm^2) of birds is accurately described by Meeh's formula (Drent & Stonehouse 1971): $S = 10 w^{2/3}$, where w is body weight in gram. The exponent is slightly lower than those found both for BMR (0.71-0.73) and for flight (0.69-0.70) (Kendeigh et al. 1977).

Within the same species, the more efficient fat deposition in larger than in smaller birds may, however, illustrate a size-related dominance. The dominance of the larger male Great Tit, Parus major, over the smaller female in winter time, with a probable influence upon the diurnal fat accumulation and corresponding nocturnal survival, has been assumed to contribute to the slightly higher survival rate in males (56%) than in females (48%) (Perrins 1979). In Falconiformes, with its reverse sexual size dimorphism, the dominance roles are reversed (Smith 1980). The habitat separation between male and female American Kestrels, where males occupy inferior habitats, has been interpreted as a result of female dominance (Mills 1976). This habitat separation

TABLE 10

Relative properties of male and female plumages in the Common Buzzard. Body weights are from Piechocki (1970), plumage weights estimated from Turcek's (1966) equation, and body surface estimated from Meeh's formula.

	Mean body weight (g)	Weight of plumage (g)	Body surface (cm ²)	Plumage weight per unit surface area (g/cm ²)
Male	790	51	874	0.058
Female	990	63	1016	0.062

combined with a slightly higher fasting metabolic rate in males compared to females may account for the differential mortality found in this species (Shapiro & Weathers 1981). For raptor species like the Common Buzzard, where both sexes defend a common winter territory, the female dominance may result in a more efficient fat deposition brought about by subtle differences in habitat use within the territory, where the female, by virtue of her larger size, is able to exclude the male from the most profitable perching sites.

In birds, however, large individuals may also benefit from their superior insulative plumage compared to smaller individuals (Kendeigh 1970). Since plumage weight approximately shows a linear relationship to body weight ($w^{0.95}$, Turcek 1966), larger birds have proportionally more plumage per unit surface area ($w^{0.67}$) than smaller individuals. For the Common Buzzard this indicates that females possess an approximately 7% better insulation than males (Tab 10).

CONSEQUENCES OF DIFFERENT TIMING OF BREEDING ON SURVIVAL

In southern Sweden, the Common Buzzard initiates breeding at a time of the year when the abundance of one of its main prey species, the Field Vole, Microtus agrestis, is actually decreasing (Fig 9). The close timing of reproduction in relation to spring temperature (Sylvén, this thesis) strongly indicates that buzzards, like several other bird species (see e.g. Perrins 1970), start breeding as soon as the environmental conditions such as food availability allow them to do so. But why do they not postpone egg laying to a more favourable period later in

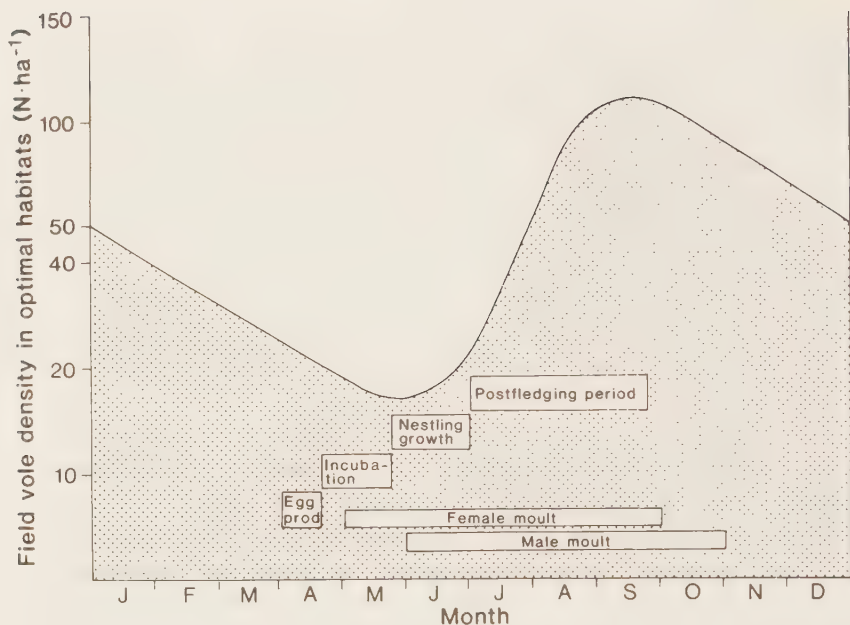


Fig.9. Timing of different activities in the Common Buzzard in southern Sweden in relation to the variation in Field Vole, *Microtus agrestis*, density in optimal habitats (data from L. Hansson, unpubl.).

spring when the vole population has begun to increase again due to reproduction and when young Rabbits, *Oryctolagus cuniculus*, have emerged from their burrows?

One factor we have to consider is the timing of moult and how it may influence survival. The importance of timing of moult in birds has been carefully examined in the Bullfinch, *Pyrrhula pyrrhula*. In both adult and juvenile Bullfinches, survival was found to be adversely affected by late moulting (Newton 1966).

To postpone egg formation until the period of rapid increase in prey abundance would delay the start of breeding until the middle of May (Fig 9). If this involves a delay of moult from the beginning of May to mid-June in females and from the beginning of June to mid-July in males, without a corresponding change in the duration of moult, it would increase the daily energy expenditure of females in October and November by a total of 55 Kcal and for males in November and December by 47 Kcal (Tab 11). In both sexes, about two thirds of this increase refers to the direct cost of moult and the rest to an increased cost for ther-

TABLE 11

Estimated differences in daily energy expenditure (DEE) in male and female Common Buzzards during late autumn due to a postponement of the start of breeding to the second half of May and the corresponding delay of moult and increased cost of thermoregulation. The activity level is supposed to remain unchanged.

Sex	Period	EM (Kcal/day)	Moult (Kcal/day)	Flight (Kcal/day)	Estimated DEE (Kcal)	"Observed" DEE (Kcal)	Difference in DEE (Kcal)
Male	Oct	128	19	9	156	156	-
	Nov	134	19	16	169	138	31
	Dec	132	10	11	153	137	16
Female	Oct	145	24	9	178	142	36
	Nov	146	12	16	174	155	19
	Dec	143	-	11	154	154	-

moregulation. Assuming an efficiency of 75% when synthesizing fat and a value of 9.5 Kcal per gram fat (Ricklefs 1974), the increase in energy expenditure will correspond to a decrease in fat accumulation of 112 g in males and 134 g in females. The delay of breeding and the corresponding postponement of moult therefore would diminish the total fat accumulation in males by approximately 86% and in females by 73%. Since fat reserves are essential for winter survival, such a decrease might jeopardize the life expectancy seriously, especially in males.

The low frequency of renesting after breeding failures found among sedentary populations of the Common Buzzard (e.g. 3% in Scotland, Picozzi & Weir 1974) may be indicative of the close interplay between the timing of breeding and the timing of moult. It is probably not pure chance that non-breeding and first year buzzards commence moulting already in spring, well before most breeding birds (pers.obs.).

The nominate form of Buteo buteo is characterized by a so called "leap-frog" migration, i.e. populations breeding in northerly areas winter south of populations of a more southerly origin (Salomonsen 1955). Those individuals experiencing the shortest breeding season are able to locate a substantial part of their moult to areas with less stressful climatic conditions. The most extreme example of this pattern is exhibited by Buteo b. vulpinus. This subspecies starts its moult in the Eurasian breeding area, interrupts it during migration, and continues it after the arrival in the South African wintering quarters (Broekhuysen & Siegfried 1970). Here it faces favourable climatic and food conditions during the austral summer with no need to accumulate fat to buffer periods of low prey accessibility due to snow cover etc. These buzzards do not even undergo a pre-migratory fattening. They gain less than 10% in weight during the whole winter stay (Broekhuysen & Siegfried 1971), presumably because they are able to cover their needs during migration by hunting on those occasions, especially during morning and evening hours, not available for thermal soaring (Alerstam 1981).

Two other examples of moult strategies found among west-palae-arctic members of the genus Buteo are given in Table 12. The northern Rough-legged Buzzard, Buteo lagopus, is probably forced to perform most of its moult in a rather short time on the breeding grounds since the climatic conditions in the winter quarters are

TABLE 12

Different moulting strategies documented for western palearctic members of the genus *Buteo*. Data on the duration and timing of moult is based on Cramp et al. (1980).

Species/subspecies	Breeding area	Winter area	Climate in the winter area	Moult period and geographical location
<i>Buteo b. buteo</i>	Boreal and temperate zone	Temperate and northern Mediterranean zone	Occasionally severe in the northern range, milder in the south	Five months, mainly in the breeding area during summer and early autumn
<i>Buteo b. vulpinus</i>	Boreal zone	Sub-Saharan Africa including savanna, steppe, and tropical winter-dry areas	Favourable	Five months, starting in breeding area, interrupted during migration, completed in winter area
<i>Buteo lagopus</i>	Mainly the tundra zone but to some extent in the boreal zone	North-eastern temperate zone, southern boreal zone, and northern steppe zone	Severe	Four months on the breeding grounds in summer and early autumn
<i>Buteo rufinus cirtensis</i>	Mediterranean and steppe zone	Mediterranean and steppe zone	Favourable	The whole year in the breeding areas

too severe to allow moulting. The north African subspecies of the Long-legged Buzzard, Buteo rufinus cirtensis, on the other hand, is not obliged to confine moult to any particular season because of the rather favourable climate in which it spends the whole year.

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THE SIGNIFICANCE OF COURTSHIP FEEDING IN THE COMMON BUZZARD,
Buteo buteo

In many bird species, the female is fed by her mate at least in the early part of the reproductive period. This behaviour, generally termed courtship feeding, was at first interpreted as being mainly a "symbolic display" to maintain bonds between the pair (Lack 1940). Royama (1966) was the first to point out its nutritional value, especially in connection with egg formation and incubation. Both in the Blue Tit, Parus caeruleus, and in the Great Tit, Parus major (Royama 1966), in the Lesser Black-backed Gull, Larus fuscus (Brown 1967a), and in the Spotted Flycatcher, Muscicapa striata (Davies 1977), the male's contribution has been found to be a substantial part of the laying female's food intake. In the Common Tern, Sterna hirundo, the rate of courtship feeding was found to influence several important breeding parameters such as egg size, clutch size, and laying date (Nisbet 1973, 1977). The rate of courtship feeding also predicted the male's feeding performance at the chick stage, both in Common Terns (Nisbet 1973) and in Herring Gulls (Niebuhr 1981).

In raptors, courtship feeding has evolved in probably one of its most extreme forms; here the male is responsible for most of the hunting almost from the time of pair formation until at least the mid-nestling stage (Newton 1979). In connection with a study of Common Buzzards in southern Sweden, I found that (1) breeding success was mainly determined at the early stage (Sylvén 1982a), (2) the breeding output was directly related to the number of eggs laid (Sylvén 1982a), (3) raising young did not involve a very strenuous level of work (Sylvén 1982b), and (4) the timing of egg laying probably has evolved to allow time for moult and fattening before winter, fattening being crucial to winter survival (Sylvén 1982b). With this background, it would be especially interesting to try and assess the significance of courtship feeding for the reproductive performance in this raptor species.

METHODS

In 1975 and 1976, the activity pattern of male and female Common Buzzards in the early phase of the breeding season was studied in three buzzard territories in southern Sweden. Males were followed for a total of 89 hrs (5343 minutes) of observation and females for 76 hrs (4582 minutes). Buzzard activity was divided into three main categories: perching, soaring, and flapping flight. At the same time, I recorded whether the buzzards were hunting, defending territory, feeding mate etc. The activity was afterwards re-

TABLE 1

Calculated daily costs for egg formation in the Common Buzzard producing three eggs. The Table is based on a method proposed by Ricklefs (1974) assuming a rapid phase of growth of the ovarian follicles of 8 days (Sylvén 1982 b), a daily linear increase in volume of 2.8 % of the ovum (daily increase = $2/n(n+1)$; n = length of the period of rapid follicular development, Ricklefs 1974), an energy content per egg of 66 Kcal (mean egg weight 63 g (Sylvén 1982 b), 1.05 Kcal/g including the white (Ricklefs 1974)), an energetic efficiency of 75 % (Ricklefs 1974), and a laying interval of three days (Webs 1964).

Days before ovulation	Per cent of final weight added per day	Days before ovulation								Days after clutch initiation						Total energy cost (Kcal)
		8	7	6	5	4	3	2	1	1	2	3	4	5	6	
1	22.2								x			x				x
2	19.5							x			x			x		
3	16.7						x			x			x			
4	13.9				x				x			x				
5	11.2				x			x			x					
6	8.4			x			x		x							
7	5.6		x			x			x							
8	2.8	x			x			x								
Daily costs of one egg (Kcal)		2.5	4.9	7.4	9.8	12.2	14.7	17.1	19.5							88.1
Daily costs of two eggs (Kcal)		"	"	"	12.3	17.1	22.0	26.9	31.7	14.7	17.1	19.5				176.2
Daily costs of three eggs (Kcal)		"	"	"	"	"	"	29.3	36.6	22.0	26.9	31.2	14.7	17.1	19.5	264.3

lated to the start of egg laying in each territory. Methods for assessment of the activity and for the corresponding energy expenditures are presented in Sylvén (1982b).

The activity studies also gave information about the rate of feeding in both sexes and the amount of prey the males delivered to their mates. To be able to relate the activity pattern and feeding efficiency to the cost of egg formation, a method proposed by Ricklefs (1974) was used. Details about the underlying assumptions of this method, and about the parameters used, are presented in Table 1 together with the estimated costs expressed on a daily basis.

RESULTS

ACTIVITY PATTERN OF MALES AND FEMALES

Table 2 presents the time devoted to different activities and the calculated costs for male and female Common Buzzard before, during, and after clutch initiation. The first five days precede the start of egg formation while the following three periods correspond to the phase of egg formation. The last two periods refer to the behaviour and energy costs at the beginning of incubation. During the first 20 days, males spent most of their flapping flight hunting (Tab 3). For soaring flight (Tab 3), most of the time was considered to be connected with movements between perching sites within the territory, but soaring no doubt also had an advertising function (Weir & Picozzi 1975). Most female flight activity took place at the early stage of the period, when thermal soaring, often together with the male, acted both as a pair contact behaviour and as a territory announcement. Female flight activity almost ceased about one week before the start of egg laying.

THE DEVELOPMENT OF COURTSHIP FEEDING

In the early part of the breeding season, males and females were often seen together hunting in the same area. When the male caught a prey, the female, by actually attacking him, forced the male to hand it over. At this stage, however, females also hunted for themselves and caught most prey on their own.

Approximately two weeks before egg laying, the males started to feed their mates more frequently. During most of the ensuing courtship feeding period, the females perched close to their nest sites and begged loudly, using a call almost identical to the begging calls of the nestlings (cf. Weir & Picozzi 1975). This feeding

TABLE 2

Calculated daily energy expenses and percentage time devoted to different activities (in brackets) in male and female Common Buzzards on a five day basis during the early part of the breeding season. To relate the activity to different ambient temperatures, the median start of laying, i.e. 15 April, found for the entire period 1975-1980 in the study area was used. Further details are given in Sylven (1982 b).

Period	Mean ambient temp.	Average activity temp. period	Male				Female			
			Diurnal and nocturnal resting	Flapping flight	Soaring flight	Total	Diurnal and nocturnal resting	Flapping flight	Soaring flight	Egg production
	(°C)	(min)	(Kcal)	(Kcal)	(Kcal)	(Kcal)	(Kcal)	(Kcal)	(Kcal)	(Kcal)
APR, 1-5	3.9	851	124 (79.9)	19 (2.2)	43 (17.9)	186	140 (86.4)	15 (1.8)	28 (11.8)	-
" , 6-10	3.4	874	124 (81.0)	37 (4.3)	35 (14.6)	196	141 (91.4)	14 (1.6)	17 (7.0)	9
" , 11-15	5.2	897	122 (86.7)	33 (3.9)	22 (9.3)	177	138 (98.4)	4 (0.4)	3 (1.2)	27
" , 16-20	5.0	919	122 (86.6)	30 (3.5)	24 (9.9)	176	138 (98.8)	4 (0.4)	2 (0.8)	17
" , 21-25	6.8	941	119 (86.6)	25 (2.9)	25 (10.6)	169	136 (98.3)	3 (0.3)	3 (1.4)	-
" , 26-30	6.5	963	120 (86.2)	26 (3.0)	26 (10.8)	172	136 (98.3)	3 (0.3)	3 (1.4)	-

TABLE 3

Proportion of time spent in flapping and soaring flight on different activities in male Common Buzzards during the period 15 days before to 5 days after clutch initiation.

	Flapping flight	Soaring flight
Hunting	78.1 %	87.1 %
Territory defence	13.4 %	2.2 %
Territory announcement	4.1 %	10.4 %
Mate feeding, mating	3.8 %	0.2 %
Nest building	0.6 %	0.1 %

of the female coincided with her egg formation. The rate of prey delivery reached a peak corresponding to the calculated maximum energy needs for egg production (Fig 1). At this time, the females had reduced their flight activity to a minimum and did not hunt at all (Fig 1).

EFFICIENCY OF COURTSHIP FEEDING

The kind of prey delivered to the females could be determined in 18 cases. In eight it consisted of voles, probably Field Voles, Microtus agrestis, and in the remaining 10 of frogs. To find out whether the male could cover the female's needs or not, some Rana arvalis and R. temporaria were collected and dried at 60°C, whereupon their energy content was determined in an Adiabatic Bomb Calorimeter (Tab 4). Since Rana temporaria was the most abundant frog in the territories studied (J. Loman, pers.comm.), this species was assumed to make up the vast majority of frogs brought to the females. Their mean energy content was estimated at approximately 25 Kcal (Tab 4). With an average body weight of 30 g and and a caloric value of 1.46 Kcal per gram fresh weight (Hansson & Grodzinski 1970), a Field Vole contains about 44 Kcal. The 18 prey-items fed to the females therefore correspond to 598 Kcal. Assuming the observed proportions of voles and frogs being typical and with an assimilation efficiency in raptors of 82% (Koplin et al. 1981), an average prey would contribute about 27 Kcal. The maximum rate of prey delivery amounted to 0.44 items per hour

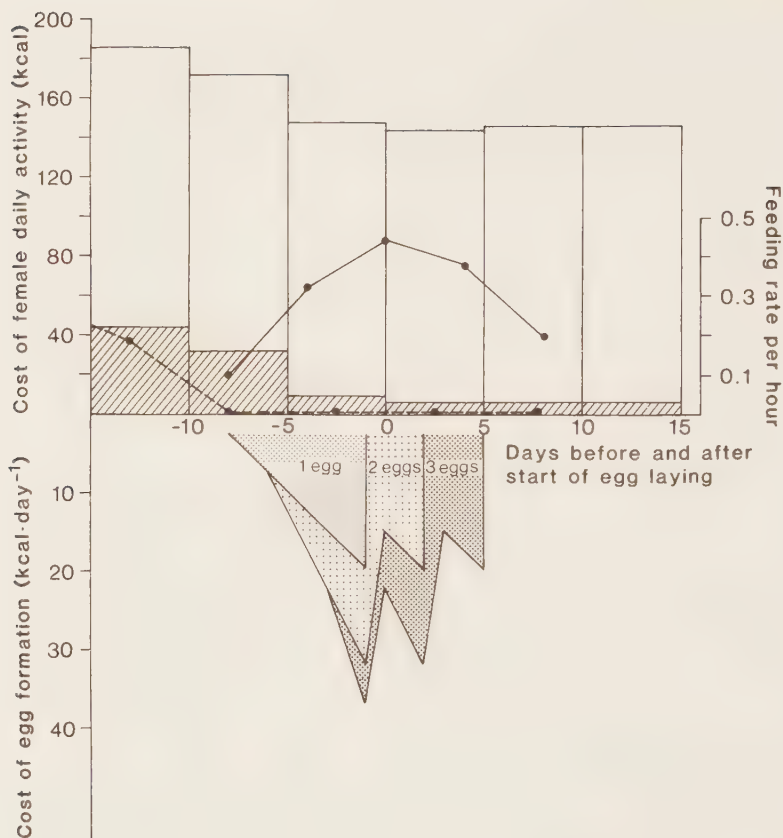


Fig.1. Female daily energy expenditure, cost of flight activity (striped area), and capture rate (dashed line) in relation to estimated cost of egg formation (from Tab.1) and the rate of prey delivery from the male (unbroken line).

(Fig 1). An activity period of about 900 minutes (Tab 1), assuming a constant feeding rate during the day, would result in 6.75 prey per day, corresponding to approximately 182 Kcal. This is slightly higher than the calculated need of the female, 172 Kcal (Tab 2).

These rough calculations indicate that the male Common Buzzard is able to cover the whole need of the female during the period when the cost of egg formation is maximal, but the margins seem to be narrow. But if he, as has been demonstrated in Blue Tits (Krebs 1970), Spotted Flycatchers (Davies 1977), and Common Terns (Taylor 1979), also selected larger and heavier prey than usually taken in order to feed the female, was not assessed in this study.

TABLE 4

Energy content and mean body weight of Rana arvalis and R. temporaria collected in southern Sweden in spring 1975.

	Kcal/g dry weight	Kcal/g wet weight	Mean weight (g)	Kcal/ prey
R.arvalis	4.58 (4.32-4.76, n = 3)	1.02 (0.99-1.06, n = 3)	13.1 (n = 27)	13.4
R.temporaria	4.45 (4.23-4.63, n = 3)	0.88 (0.86-0.90, n = 3)	28.0 (n = 18)	24.6

DISCUSSION

To store sufficient amounts of energy and protein for egg formation, a female could adopt one of two strategies: (1) increase her foraging time and effort, (2) rely on the male to supply her with the necessary food while remaining more or less inactive herself, or combine the two (Reynolds 1972).

Most raptor females have adopted the second strategy. But if the availability of food indeed limits clutch size, as has been suggested for the Common Buzzard (Sylvén 1982a), it might be asked why the female stops feeding for herself at the time when her requirements appear to be largest. In the Common Tern, it has been suggested that the extra burden of the eggs and the reproductive organs decreases the female's foraging efficiency to such a degree, that it is more economical for her to rest and rely on the male for food (Nisbet 1977). This could apply to gulls and terns, which have exceptionally heavy clutches in relation to adult body weight, but hardly to raptors. In hawks and owls an egg is only about 6.5% of adult weight compared to 15.6% in gulls and terns (Ricklefs 1974). Raptors are also characterized by a prolonged laying period with an average laying interval of three days (Ricklefs 1974) which further reduces maximum load. Using weight data for the Common Buzzard from Piechocki (1970), the weight increase due to the development of the reproductive organs was calculated at about 66 g. The maximum load due to the eggs (on the day before the first egg is laid) was calculated to be

118 g (from Tab 1). This extra load of 184 g would increase the cost of flight (calculated according to Kendeigh et al. 1977) by no more than 14 per cent.

Indeed it would be more profitable for the female to hunt by her own also during the egg formation period, provided that the male continues feeding her. Seventy-eight per cent of the male's time in flapping flight is spent on hunting (Tab 3). By this effort he covers both his own needs and those of the female, which are approximately similar (Tab 2). Therefore, if a female hunted for herself during a time corresponding to half the hunting time of the male, she would, with a cost of about 13 Kcal ($33 \times 0.78 \times 0.5$; see Tabs 2 & 3), add some 180 Kcal per day to the energy received from the male. This net gain of 167 Kcal corresponds to the cost of forming about two eggs (Tab 1) or of accumulating about 13 g fat (with an efficiency of 75% and a value of 9.5 Kcal per gram fat, Ricklefs 1974). This fat could be used as an insurance against an inability of the male to provide sufficient amounts of food during incubation. To refrain from such profits, the female must certainly have strong reasons. We therefore have to seek for other explanations why the female stops hunting at this stage of the breeding.

Two ultimate reasons for the evolution of courtship feeding have been suggested, both of which are applicable to raptorial birds. For birds with a predatory life-style and where hunting requires powerful strikes against the prey, courtship feeding could eliminate the considerable risk of destroying the developing eggs within the female's body (Walter 1979). This applies not only to diurnal and nocturnal raptors, but also to skuas, gulls, terns and kingfishers, groups where courtship feeding is significant at or just prior to clutch completion (Andersson 1971, Brown 1967, Niebuhr 1981, Nisbet 1973, 1977, Glutz & Bauer 1980) and whose hunting techniques are similar to those of raptors.

Courtship feeding also enables birds to reduce the exposure of the eggs to predation or to overheating (Hunt 1980). This refers to open-nesting species with conspicuous nests like most raptors, to gulls and terns breeding in colonies, to skuas, but hardly to kingfishers (concealed nesting habits, small body sizes). No doubt, predation is of considerable importance in all these forms, including raptors. In the Herring Gull, predation both at the egg stage (Brown 1967b) and nestling stage (Parson 1971, 1976) accounts for a substantial part of the losses, and in the Long-

tailed Skua, Stercorarius longicaudus, egg losses, although few, were associated with predation (Andersson 1976a), which also was suggested to be the ultimate factor determining clutch size (Andersson 1976b). In terns, where predation sometimes is considerable (Lemmetyinen 1971), and in gulls, colony breeding has been found to lessen the predation rate, at least for pairs nesting in the centre of the colony (Kruuk 1964, Patterson 1965).

Due to their predatory habit and large body size, raptors probably are better suited than most birds for nest defence. Nevertheless, raptors are vulnerable to predation, where small hole-nesting species suffer least, raptors which use open trees or cliffs are intermediate, while those which nest on the ground suffer most losses (Newton 1979). In this group, as well as in gulls, terns and skuas, the ultimate cause of nest failure is often food shortage while predation works as the proximate factor. Therefore, courtship feeding is valuable to prevent such losses.

In hole-nesting insectivorous birds like tits, where feeding hardly exposes the female's developing eggs to any substantial danger and where the risk of predation on the eggs in the nest, which the birds themselves have scant ability to protect due to their small body size, seems to be rather insignificant (see e.g. Perrins 1979), the female can afford to forage on her own. Thereby, she is able to cover her own maintenance costs, while she at the same time is being fed by her mate, who sometimes provides energy corresponding to the cost of egg formation (Royama 1966).

These observations illustrate the significance of predation as a selective factor acting on the behaviour of many open nesting species; courtship feeding being only one important adaptation to avoid it. But the calculations for the Common Buzzard also demonstrate that the necessity for courtship feeding can have considerable disadvantages with regard to egg production, and that the buzzards therefore also are vulnerable to changes in the environment, such as the availability of food, early in the breeding season.

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Interspecific relations between sympatrically wintering Common Buzzards *Buteo buteo* and Rough-legged Buzzards *Buteo lagopus*

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Sylvén, M. 1978. Interspecific relations between sympatrically wintering Common buzzards *Buteo buteo* and Rough-legged Buzzards *Buteo lagopus*. — *Ornis Scand.* 9: 197-206.

(1) Food and habitat utilization, activity and territorial behaviour in the Common Buzzard *Buteo buteo* L. and the Rough-legged Buzzard *B. lagopus* Pontopp. were studied in southern Sweden where the two species winter sympatrically.

(2) Both species maintained virtually exclusive territories both intra- and interspecifically.

(3) The species showed nearly identical food choice, and the overlap value was calculated to be 0.99. The Common Buzzards were, however, found to take slightly more *Apodemus* spp than the Rough-legs.

(4) Habitat distribution of the two species was very similar, and the overlap was found to be 0.88, but the Common Buzzards perched (i.e., looked for prey) more often in groves and swamps and less often in moist and dry meadows than the Rough-legs. However, both species preferred to hunt in areas with high rodent densities and avoided the poorer habitats.

(5) Rough-legged Buzzards were found to hover to some extent, especially in strong wind, while the Common Buzzards did not make use of this hunting technique or at least only very rarely. Calculations of the power requirement in both species showed, however, that the Common Buzzard would require less energy for hovering than the Rough-legs. The hunting success of hovering Rough-legs indicates that hovering is an expensive method to obtain rodents except under high wind velocities. Since both species in most cases hunt using a "sit and wait strategy" the species compete for suitable perching sites.

(6) The diel periodicity in both species was found to be almost identical with a flight activity peak around noon.

(7) Because of the great ecological similarities between the two species it seems adaptive for them to defend territories both intra- and interspecifically. The largely separate winter distribution of the two species suggests that individuals of both species have higher fitness when they do not have to compete with members of the opposite species.

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Introduction

Both breeding areas (Fig. 1) and winter ranges (Fig. 2) of the Common Buzzard *Buteo buteo* L. and the Rough-legged Buzzard *B. lagopus* Pontopp. are mainly allopatric, but in some parts of central and eastern Europe and in southern Scandinavia the two species winter sympatrically. The Rough-legged Buzzard in

most years is a rare winter visitor in, for example, southern West Germany, Holland, and Belgium, where, however, its abundance varies strongly between years and it may be classified as an irruptive migrant (Schüz 1945, Ulfstrand 1963, Scott 1968). It is more abundant in Hungary, East Germany, and Poland (Glutz von Blotzheim et al. 1971). The number of Rough-legged

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Fig. 1. Breeding distribution of the Common and Rough-legged Buzzard on the Scandinavian peninsula (after Haftorn 1971). The gap between the ranges is not total, but both species are very scarce in that zone.

Buzzards compared to the number of Common Buzzards becomes progressively higher from western to eastern Poland, the former species making up only 10–15% of the total number of buzzards in western Poland, while further east both species are equally common during the winter or, occasionally, the Rough-legged Buzzard is more abundant (Truszkowski 1976). The main migratory direction of Scandinavian Rough-legs is south to southeast (Haftorn 1971, Schüz 1971) in contrast to Scandinavian Common Buzzards which winter mainly in southwestern Europe (Olsson 1958).

As the species are congeneric, resemble each other in morphology and size, and have roughly the same food habits one is prompted to ask what behavioural and ecological differences enable the two species to coexist. No study of this problem has been conducted in the Palaearctic, but in North America the interspecific relationships between wintering Rough-legs and Red-tailed Buzzards *Buteo jamaicensis* Gmelin have been examined in several areas (Craighead and Craighead 1969, Schnell 1968).

The purpose of this paper is to present some data on food and habitat utilization, activity and territorial behavior among Common and Rough-legged Buzzards wintering sympatrically in southern Sweden and, on the basis of these data, to discuss the problem of how they can coexist for extended periods of time.

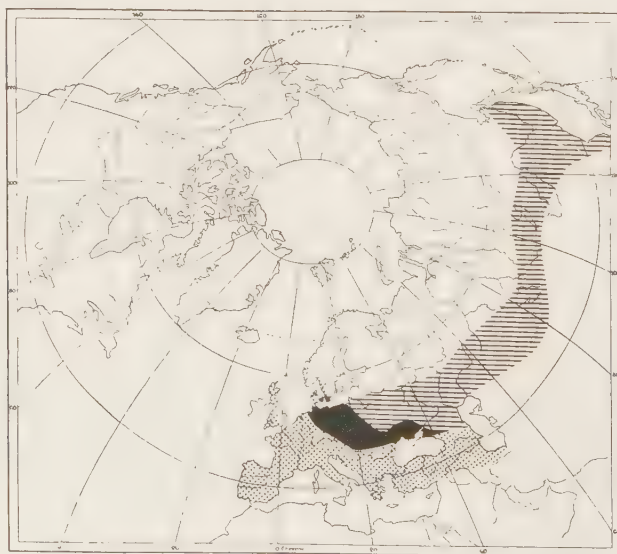


Fig. 2. Winter distribution of the Common Buzzard (dotted) and of the Rough-legged Buzzard (striped) and their zone of overlap (black) in the Palaearctic (mainly after Dement'ev et al. 1966).

Study area and methods

The study was carried out between October and March 1975/76 in a 12 km² area in southern Sweden (55.42N, 13.25E). The habitats consisted of grassland, marshes, and swamps with groves.

Food habits were determined by analysis of pellets which were collected monthly at roosts within the study area.

Habitat utilization was recorded by plotting perching sites on a map. Six different habitat categories were distinguished: (1) groves consisting mainly of *Betula* spp, *Alnus glutinosa* L., and *Pinus silvestris* L. (on drier ground), (2) marshes with *Carex* spp., and *Salix* spp, (3) swamps with rich vegetation of *Urtica dioica* L., *Filipendula ulmaria* L., and *Epilobium hirsutum* L., (4) moist meadows with *Deschampsia caespitosa* L., (5) intermediate meadows with *Dactylis glomerata* L., and (6) meadows on dry ground with *Corynephorus canescens* L. In addition perching sites were classified as high trees (>3 m), low trees and bushes (<3 m), and high and low utility poles, respectively. Birds perching on wires close to utility poles were included in the last-mentioned categories. Observations were made from a car driving through the area with short stops when necessary for accurate identification.

The data concerning activity and territorial behaviour of both species were collected simultaneously. In most cases it was possible to watch one individual of both species at the same time. Some observations relating to the activity of the two species were, however, collected on the same day but not simultaneously. Individual identification was facilitated through wingtags on five Common and one Rough-legged Buzzard, while plumage features were clear enough to allow individual recognition in the remaining cases, since both species but especially the common Buzzard are highly variable with respect to plumage pattern and colouration (Ulfstrand 1977). During the activity studies, perching sites, movements of each individual, and places where overt aggression events occurred were plotted on habitat maps. Buzzards spend much of their time perched on look-out posts. "Perching" therefore in this paper refers to their hunting activity.

Results

The food items in the regurgitated pellets are listed in Tab. 1. Although both species subsisted chiefly on *Microtus agrestis* L., the proportion of this prey in the diet of the Rough-legs was higher than in that of the Common Buzzard ($\chi^2 = 6.00$, $p < 0.05$). On the other hand, Common Buzzards took significantly more *Apodemus* spp than did the Rough-legs ($\chi^2 = 14.07$, $p < 0.001$).

Some differences occurred in the behaviour of Common and Rough-legged Buzzards in the various habitats (Tab. 2). The Common Buzzards perched significantly more often in groves and swamps and the Rough-legs in moist and dry meadows. Common Buzzards showed a greater preference ($\chi^2 = 17.86$, $p < 0.001$) for higher perches and a slightly greater preference ($\chi^2 = 4.28$, $p < 0.05$) for trees than did Rough-legs (Tab. 3). No significant differences were found between the use of utility poles ($\chi^2 = 0.46$), while Roughlegs perched more often on the ground ($\chi^2 = 45.15$, $p < 0.001$) than did Common Buzzards (Tab. 3).

Data on the daily activities of the two species are given in Tab. 4 and Fig. 3. The foraging behaviour was different between the species in only one respect, the Rough-legged Buzzards hunting significantly ($\chi^2 = 5.98$, $p < 0.05$) more often by hovering. This behaviour was not seen in the Common Buzzards during the study periods, but on some other occasions Common Buzzards were seen hovering, though only for brief moments and exclusively in strong wind.

Tab. 1. Number and proportion of different prey categories in pellets of the Common and Rough-legged Buzzard collected from November to March.

Species	<i>Buteo buteo</i>	<i>Buteo lagopus</i>
<i>Microtus agrestis</i> L.	170 (81.7%)	183 (90.1%)
<i>Arvicola terrestris</i> L.	2 (1.0%)	2 (1.0%)
<i>Apodemus</i> spp.	19 (9.1%)	2 (1.0%)
<i>Sorex</i> spp.	4 (1.9%)	8 (3.9%)
<i>Talpa europaea</i> L.	2 (1.0%)	4 (2.0%)
<i>Oryctolagus cuniculus</i> L.	5 (2.4%)	3 (1.5%)
<i>Aves</i> spp.	6 (2.9%)	1 (0.5%)
Total	208	203

Tab. 2. Number and proportion of observations of Common and Rough-legged Buzzards perching in different habitat categories.

Habitat	<i>Buteo buteo</i>	<i>Buteo lagopus</i>	χ^2 , p-value
(1) Groves	102 (9.6%)	12 (3.4%)	13.45, $p < 0.001$
(2) Marshes	127 (12.0%)	37 (10.6%)	0.47, $p = 0.49$
(3) Swamps	240 (22.6%)	28 (8.0%)	36.27, $p < 0.001$
(4) Moist meadows	185 (17.4%)	121 (34.7%)	46.02, $p < 0.001$
(5) Intermediate meadows	347 (32.2%)	116 (33.2%)	0.04, $p = 0.84$
(6) Dry meadows	61 (5.7%)	35 (10.0%)	7.60, $p < 0.01$
Total	1062	349	

Tab. 3. Different perching sites and their utilization by Common and Rough-legged Buzzards expressed in number and proportion of observations.

Perch site	<i>Buteo buteo</i>	<i>Buteo lagopus</i>
High trees	313 (42.0%)	85 (31.4%)
High utility poles	250 (33.5%)	66 (24.4%)
Low trees or bushes	36 (4.8%)	22 (8.1%)
Low utility poles	134 (18.0%)	67 (24.7%)
Ground	13 (1.7%)	31 (11.4%)
Total	746	271
High perching sites	563 (75.5%)	151 (55.8%)
Low perching sites	170 (22.8%)	89 (32.8%)
No. of trees used	349 (46.8%)	107 (39.5%)
No. of utility poles used	384 (51.5%)	133 (49.1%)

It appears from Tab. 4 that both species spent most of the day perched and that less than 9% of their time was devoted to other activities. Both seemed to maximize their non-perching activity around noon (Fig. 3). The number of observations of overt territory defense, intra- and interspecifically, are listed in Tab. 5, but expressed in time they make up only 0.3% of the species' total time budgets (Tab. 4).

In February and March Rough-legged Buzzards perched more frequently than did Common Buzzards ($\chi^2 = 5.33$, $p < 0.05$ and $\chi^2 = 16.73$, $p < 0.001$, respectively). No such differences were observed in November to January (Fig. 4; $\chi^2 = 0.10$, $\chi^2 = 2.78$, $\chi^2 = 2.92$, respectively). Especially soaring increased markedly during February and March in the Common Buzzard in association with the approaching breeding season. Males and females were, for example, often seen soaring together. This probably also explains the differences in the species' total time budget which is apparent from Tab. 4.

Common and Rough-legged Buzzards were intra-

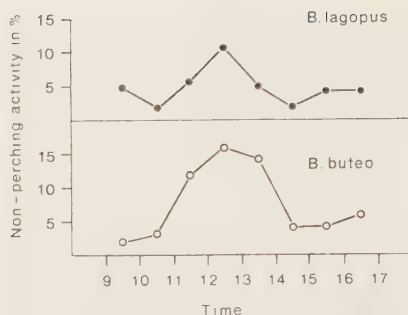


Fig. 3. Diel activities in the Common and Rough-legged Buzzard expressed as non-perching (flight) activity.

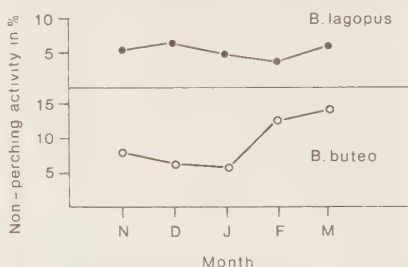


Fig. 4. Monthly distribution of non-perching (flight) activities in the Common and Rough-legged Buzzard.

and interspecifically territorial in the study area. They defended fixed areas from which intruders were excluded by aggressive behaviour. Fig. 5 shows the territorial system in the winter 1975/76. Sometimes the location

Tab. 4. Total time budgets in minutes of Common and Rough-legged Buzzards during November to March.

<i>Buteo buteo</i>	Resting	Flapping flight	Hovering	Soaring	Total
Perching and foraging	2299	50	—	33	2382 (94.9%)
Overt territory defense	—	7	—	—	7 (0.3%)
Other activities	—	12	—	107	119 (4.7%)
Total	2299 (91.6%)	69 (2.8%)	—	140 (5.6%)	2508
<i>Buteo lagopus</i>					
Perching and foraging	2353	49	38	29	2469 (99.1%)
Overt territory defense	—	7	—	—	7 (0.3%)
Other activities	—	5	—	7	12 (0.5%)
Total	2353 (94.6%)	61 (2.4%)	38 (1.5%)	36 (1.5%)	2488

of the territory boundary was difficult to determine since only a small proportion of the time was devoted to territory defense (Tab. 4) and since trespassing by neighbours fairly often occurred when the territory owners were absent. But as soon as the owners returned the intruding buzzards most often disappeared at the mere sight of the territory holders. Very seldom trespassing resulted in threats or attacks; this happened mostly when intruding individuals did not notice the arrival of the territory holders. In some cases buzzards were dominant at a perching site towards some individuals, mostly distant neighbours, but not against others. This is indicated by the slight overlaps in Fig. 5. Otherwise, borderlines between close neighbours seemed to be very clearly settled and territories were practically non-overlapping.

The territory boundaries were superimposed on the habitat map, and thus it became possible to determine the proportion of different habitat categories within each territory. In this respect only weakly significant interspecific differences were found, the territories of the Common Buzzard including slightly more groves and less dry meadows than those of the Rough-legged Buzzard (Tab. 6; Mann-Whitney's U-test, two-tailed, $p \leq 0.05$ and $p \leq 0.05$, respectively). However, it was found that both species looked for prey (perched) significantly more often in swamps and moist meadows and less often in intermediate and dry meadows than would

Tab. 5. Number of observations of overt territory defense in each species against conspecifics and individuals of the opposite species.

Territory holder	Intruder	
	<i>Buteo buteo</i>	<i>Buteo lagopus</i>
<i>Buteo buteo</i>	18	6
<i>Buteo lagopus</i>	9	1

Tab. 6. Total area in km² and their proportion of different habitat categories in 12 territories of the Common Buzzard and in 3 of the Rough-legged Buzzard.

Habitat	<i>Buteo buteo</i>	<i>Buteo lagopus</i>
(1) Groves	0.28 (7.4%)	0.02 (1.8%)
(2) Marshes	0.27 (7.1%)	0.08 (7.3%)
(3) Swamps	0.38 (10.0%)	0.03 (2.8%)
(4) Moist meadows	0.40 (10.6%)	0.21 (19.3%)
(5) Intermediate meadows ..	2.09 (55.1%)	0.43 (39.4%)
(6) Dry meadows	0.37 (9.8%)	0.32 (29.4%)
Total	3.79	1.09

have been the case if the birds had exploited the different habitats in proportion to their availability in the area (Tab. 7). Since the former two types are known to support about three times as dense populations of *Microtus*



Fig. 5. The winter territories of locally breeding pairs (striped) and of immigrant individuals (dotted) of the Common Buzzard, and of the Rough-legged Buzzards (open) wintering in the study area in 1975/76. Wooded areas are black

Tab. 7. Number of observations of perching Common and Rough-legged Buzzards in different habitat categories compared to the expected numbers calculated from the proportion of the habitats within the territories of the species (see Tab. 6).

Habitat	<i>Buteo buteo</i>				<i>Buteo lagopus</i>			
	Observed	Expected	χ^2	p	Observed	Expected	χ^2	p
(1) Groves	102	78	6.95	p < 0.01	12	6	2.05	p = 0.15
(2) Marshes	127	75	14.69	p < 0.001	37	25	2.55	p = 0.11
(3) Swamps	240	106	51.62	p < 0.001	28	10	9.02	p < 0.01
(4) Moist meadows	185	112	20.70	p < 0.001	121	67	21.23	p < 0.001
(5) Intermediate meadows	347	585	109.18	p < 0.001	116	138	29.27	p < 0.001
(6) Dry meadows	61	104	12.24	p < 0.001	35	103	41.76	p < 0.001

agrestis as the latter ones (L. Hansson, pers. comm.), both species clearly preferred habitats with a high rodent density.

Discussion

According to Cody (1974) the various means by which bird species can differ from each other in their use of resources are: (1) in food selection, (2) in habitat, (3) in vertical stratification of feeding zones, (4) in feeding behaviour, and (5) in temporal segregation within the diel cycle. To reduce interspecific competition, the two buzzard species conceivably may employ all separating mechanisms except the third.

Food and habitat selection

The extent of ecological overlap between the Common and Rough-legged Buzzard in terms of food and habitat selection was calculated using Pianka's (1973) formula, at 0.99 and 0.88, respectively. The two species hence were more segregated by habitat than by food. The larger proportion of *Apodemus* spp in the diet of the Common Buzzard probably reflects this slight habitat specialization as this species was found to perch (hunt) significantly more often in groves than the Rough-legged Buzzard. Both *Apodemus* species in the study area are found in woodland, but while *A. flavicollis* Melchior is almost completely restricted to this habitat, *A. sylvaticus* L. occurs both in woodland and grassland (Hoffmeyer 1973).

Schnell (1968) found Rough-legged Buzzards to be more active than Red-tailed Buzzards, but there was no significant difference in field type preference between the species. The Red-tailed Buzzard which can be regarded as a Nearctic ecological equivalent to the Common Buzzard (Brown and Amadon 1968) did show a greater preference for trees and, especially, relatively tall trees than did the Rough-legs. The Red-tailed Buzzard also perched more often in groups of trees or groves whereas the Rough-legged Buzzards more often were found in lone trees. Schnell concluded that this partial subdivision of "the available living space" by using different perch types resulted in the species ex-

ploting different areas and prey populations and consequently in a reduction of competition.

Craighead and Craighead (1969) also found the Rough-legs to be more active than the Red-tailed Buzzards, but the perching height most frequently used by the two species was about the same. The red-tailed Buzzards frequented woodlots more often than did the Rough-legs as well as wetter areas.

Both Schnell's and the Craigheads' results correspond to the situation found in this study. Like the Red-tailed Buzzards, the Common Buzzards perched more often in groves and trees and on higher sites than the Rough-legs. They more often exploited wetter areas and less frequently dry ones than did the Rough-legs.

Feeding behaviour

Both species perched most of their time, but the Rough-legs sometimes hunted using hovering flight, even though this behaviour took up only a small fraction of their time (1.5%). To what extent can this special hunting technique be instrumental in reducing the competition between the Rough-legs and the Common Buzzards?

Hovering flight allows a bird to exploit areas lacking suitable perching sites, and if the Rough-legs were to use this behaviour extensively, it would be possible for them to exploit areas less available for the Common Buzzards which, according to my results, depend on perching sites to a larger extent. But hovering is a most power-demanding type of activity being, for example, much more expensive than ordinary flapping flight (Weis-Fogh 1972). Pennycuik (1975) gives an equation for the power requirement of hovering. According to this the Common Buzzard requires less power input (121.0 W; body mass = 0.890 kg, wing span = 1.2 m, air density = 1.22 kg/m³, muscle or mechanical efficiency = 0.23) than the Rough-legged Buzzard (131.1 W; body mass = 1.048 kg, wing span = 1.4 m, air density and muscle efficiency as above).

Since both species exploit similar prey species, the reward per prey is almost the same, and if their hunting success is similar, Common Buzzards would be expected to hover at least as often as Rough-legs. According to the calculations it would even be energetically more fa-

avourable for Common Buzzards to hover than for Rough-legs.

Hansson and Grodziński (1970) measured the mean body mass (0.021 kg) and the calorific content (1.46×10^3 Kcal/kg) of *Microtus agrestis* from the study area during autumn. During the activity studies the Rough-legs were found to catch only two rodents (each worth about 129 KJ) in 38 min when hovering. This energy reward (258 KJ) will not even suffice to pay for the energy expenditure of hovering flight (299 KJ). But the energy consumption of hovering is reduced due to the kinetic power of the wind. It is mechanically equivalent for a bird to fly in calm air at a given speed or to fly against a headwind with the same airspeed and then being stationary in relation to the ground (Pennycuik 1975). The power requirement of flying birds is reduced with increasing flight speed at low velocities until a minimum value after which the metabolic effort increases with increasing speed. Power input during flight for both species at the minimum power speed (9–10 m/s) was found to be about half as energy consuming as the power requirement for hovering in calm air (minimum power input for the Rough-legged Buzzard 57.8 W and for the Common Buzzard 55.1 W). Hence even moderately strong winds would probably make the hovering hunting technique more profitable for both species. It is therefore of interest to note that such an increase in flight and hovering activity with increasing wind velocities was recorded by Schnell (1967) for the Rough-legged Buzzard.

But why both species do not hover to the same extent is unclear. An aerodynamic explanation might be that the "maximum power output continuously available" (Pennycuik 1972, 1975) is relatively larger in the Rough-legged Buzzard than in the Common Buzzard. This would mean that the former species could hover at lower wind velocities than the latter. This assumption would be fulfilled if the power available per unit mass of flight muscles is larger in the Rough-legged Buzzard than in the Common Buzzard or if the flight muscles of the Rough-legged Buzzard are proportionately larger than in the Common Buzzard (assuming the available power per unit of flight muscles to be roughly the same in both species). As a matter of fact, the only available data from the literature (Greenewalt 1962) indicate that there is no difference. About 19.7% of the body mass consists of pectoralis muscles in the Common Buzzard and 20.5% in the Rough-legged.

Since I can find no trace of any aerodynamic superiority in the Rough-legged Buzzard in relation to the Common Buzzard, I suggest the difference in hovering frequency between the species during winter to reflect a behaviour evolved and useful on their breeding grounds, where the Common Buzzard generally occupies wooded areas unsuitable for using the hovering hunting technique while the Rough-legged Buzzard is a bird of the open tundras.

In the absence of strong wind the Rough-legs in the

study area preferred to practise a "sit and wait strategy" and hence became dependent on favourable perching sites like the Common Buzzards. The slight segregation in feeding behaviour therefore probably was of minor importance in reducing the competition between the species.

Temporal segregation

My data demonstrate no interspecific segregation in activities within the diel cycle. Both species seemed to perch less frequently around noon. The hunting periodicity may be influenced by the activity of the voles. Thus *Microtus agrestis*, the main food component of both species, has a pronounced activity peak during the afternoon and early evening and a smaller peak at sunrise, at least in November and December (Hansson and Grodziński 1970).

Territoriality

The Common and Rough-legged Buzzards are very similar with respect to diel activity, hunting behaviour, food, and habitat distribution. The most pronounced interspecific difference in my study area seemed to be in terms of habitat segregation, but are differences in habitat selection of this magnitude enough to avoid severe competition between the species in sympatry?

If individuals compete for a resource such as food, spacing becomes of adaptive value as it leads to reduced pressure on the critical resource (Brown 1975). Most birds defend territories only against conspecifics, but in some cases also against individuals of other species, usually closely related ones (Simmons 1951, Orians and Willson 1964, Cody 1969, Murray 1971).

In the study area both single individuals and pairs of the Common Buzzard defended fixed areas. The winter range of locally breeding pairs was situated in the same area as in the previous and/or following breeding season. Sometimes winter and summer ranges were identical, but in some cases a pair defended only a limited part of the breeding territory. This corresponds to a situation found in Britain by Weir and Picozzi according to Brown (1976). Mutually exclusive territories were, however, not found by the Craigheads (1969), who concluded that the activity ranges of all *Buteo* species, viz. The Red-tailed, the Rough-legged, and the Red-shouldered Buzzard (*Buteo lineatus* Gmelin), overlapped considerably or even were completely contained within each other during the winter. There "existed a hunting tolerance which operated automatically", and each area "had a definite carrying capacity which was recognized by the hawks". Disputes occurred, but were exceptional.

The Rough-legged Buzzards in my study area also held territories. Like some of the Common Buzzards which did not breed in the study area but annually returned to the same winter territories (Fig. 4), individual

Rough-legs occupied the same territories during successive winters. Thus, one individually recognizable Rough-legged Buzzard (wing-tagged) defended the same territory in the winter of 1975/76 as in the previous three winters, and both the other territories occupied by Rough-legs had been used by that species during several years, at least in one case probably by the same individual (judging from plumage features). Such "Ortstreue" in migrants had been shown in many cases, for example, in a subspecies of the Common Buzzard (*Buteo b. vulpinus* Gloger) wintering in South Africa (Moreau 1972).

More than the slight habitat segregation between the species, the intra- and interspecific territoriality seemed to be an important mechanism enabling the species to coexist. But is the strategy of interspecific territoriality a useful adaptation to be expected among sympatric populations of two species?

Orians and Willson (1964) identified three situations in which interspecific territoriality might be expected: (1) when the structure of the habitat is simple, for example, tundra, marshland, desert, and grassland, (2) when the species are adapted to exploit stratified food resources like rodents, or (3) when several other species are already exploiting the same resources, because this prevents divergence of a species in a certain direction even in a diversified habitat. At least the two first assumptions seem to be fulfilled for the buzzards in the study area.

According to Brown and Orians (1970) the rate of capture of food items by numbers of one species will become reduced if their territories are shared with members of another competing species. This effect would necessitate an increase in average territory size or lead to reduced reproductive rates during the breeding season. Taking into account the degree of similarity between two given species, Cody (1974) calculated the advantage of being interspecifically territorial during the breeding season. He showed that the advantage of the behaviour will increase in proportion to the niche overlap.

Interspecific territoriality seems to be widely regarded as a useful adaptation between ecologically similar species, at least in structurally simple environments, and the "convergence hypothesis" presented by Cody (1969) has attracted great attention. In two publications, however, Murray (1971, 1976) has argued that mutual interspecific territoriality is maladaptive in most cases, and that the predictions of the "convergence hypothesis" are explicitly contrary to those of the competitive exclusion principle. Earlier authors (Wynne-Edwards 1962, Hamilton 1964) have also recognized that if interspecific territoriality between species occupying the same habitat is stable and has evolved by natural selection the competitive exclusion principle is contradicted.

Like Cody (1974), Murray (1971, 1976) concludes that most cases of interspecific territoriality occur in

species that are mainly allopatric and have only marginal overlaps, or in species having different habitat preferences and being interspecifically territorial only in intermediate habitats. But Murray goes further in saying that interspecific territoriality is rare or absent in widely sympatric species exclusively occupying the same habitat. He discusses numerous published cases of the behaviour and dismisses most of them, either because of lack of proper evidence or because they may be viewed as cases of aggression that has evolved in intraspecific contests and is misdirected towards individuals of the other species possessing features similar to those normally stimulating intraspecific territoriality. He further argues that because the individuals of one of two competing species usually are dominant over individuals of the other, dominance must result in interspecific divergence of, for example, habitat distribution or foraging behaviour since the subordinate species otherwise will be excluded from its optimal habitats.

If interspecific territoriality is maladaptive, selection will work against it, at least in one species. Several authors (Selander and Giller 1963, Orians and Willson 1964, Murray 1971) have, however, suggested that interspecific territoriality may still occur in narrow zones of sympatry because selection for divergence is swamped if the population at the periphery of the species' ranges, especially expanding species, are composed of immigrants from the central portions of the species' distributions where there is no selection against interspecific territoriality.

In a test of the adaptiveness of interspecific territoriality in hummingbirds, Lyon et al. (1977) found the species involved to be fully capable to distinguish between each other. The assumption of Murray that interspecific territoriality can be regarded as misdirected aggression therefore was rejected. On the other hand they found no evidence of character convergence, and they conclude that "effective adaptive interspecific territoriality can occur despite large differences in size and plumage characteristics of the interacting species".

Due to its larger size, the Rough-legged Buzzard may be socially dominant (Morse 1974), or "biologically dominant" (Hediger 1940), over the Common Buzzard. But in western Europe migrating Rough-legs have to compete against resident pairs as well as wintering migrants of the Common Buzzard. As territory holders all the year around the stationary Common Buzzards may possess an advantage in relation to the Rough-legged Buzzards. This has been demonstrated for many bird species in an intraspecific context (Hinde 1956) and might be valid also in interspecific controversies. The intra- and interspecific territorial behaviour of the resident Common Buzzards hence must cause an exclusion of the wintering migrants of both the Common and Rough-legged Buzzard from otherwise suitable habitats. But in interspecific battles between migrating birds of both species, the Rough-legged Buzzard may possess an advantage due to its larger size. The interspecific terri-

torial behaviour therefore seems to be an important adaptation when the species are wintering sympatrically. To regard this behaviour as misdirected aggression, like Murray (1971), seems unnecessary. This speaks in favour of Cody's argumentation.

However, it must be advantageous for Rough-legged Buzzards to exploit areas free from Common Buzzards and hence to avoid the interspecific competitive combat. In allopatry all favourable habitats will be accessible for the Rough-legs, and this will increase the fitness of wintering individuals of the species. This consideration speaks in favour of segregation between the species either through divergent habitat selection or through different geographic distributions.

Like their Nearctic equals (Bock and Lephien 1976), the Palaearctic Rough-legged Buzzards primarily winter in areas characterized by relatively short growing season and low precipitation. The climate in these areas is continental with low temperature and sometimes heavy snow cover. Due to its larger size the Rough-legged Buzzard probably can withstand these harsh conditions better than the smaller Common Buzzard (for discussion of the advantage of being large, see e.g. Kendigh 1969, McNab 1971, Calder 1974). And the Rough-legs' ability to hover, even though it is a relatively expensive tactic presumably adaptive mainly on the breeding grounds, may also be of significance for birds constrained to hunt in areas poor in suitable perching sites like the open plains characterizing parts of the species' wintering range.

The largely allopatric winter distribution of the Common and Rough-legged Buzzards, with relatively small areas of sympatry, reflects the competitive relationship between the species. The fact that the small numbers of Rough-legged Buzzards actually wintering in Great Britain after irruptive migrations are found mostly in southeastern England (Scott 1968) is striking since breeding Common Buzzards are nearly completely absent from that area (Sharrock 1976) and wintering Common Buzzards probably are scarce too due to the stationary habits of the British population (Tubbs 1974, Picozzi and Weir 1976). Individuals of both species probably have higher fitness when living in allopatry than in sympatry, but when in sympatry interspecific territoriality appears to be an important adaptation to the two species.

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